The Distribution and Ecology of Mammals on Leyte, Biliran, and Maripipi Islands, Philippines

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Abstract

The land mammal faunas of the Philippine islands of Leyte, Biliran, and Maripipi are described. Collectively, a total of 48 indigenous species are known to occur on the three islands: 45, 30, and 25 from Leyte, Biliran, and Maripipi, respectively. These include 1 insectivore, 1 dermopteran, 33 bats, 2 primates, 7 rodents, 2 carnivores, and 2 ungulates. All but three of these species occur on the large neighboring island of Mindanao. The exceptions include a widespread but rarely captured vespertilionid bat and two rodents that have sister-species on Mindanao. Among the remaining 45 species, 9 are restricted to the Mindanao faunal region, 10 are more widely distributed in the oceanic Philippines, and 26 have distributions that extend outside of the Philippines. One species from Biliran and two from Maripipi (all poorly known insectivorous bats) have not been recorded from Leyte. Otherwise the faunas of the two smaller islands are subsets of the Leyte fauna, which is, in turn, a subset of the Mindanao fauna. Data indicate that the present-day mammal faunas of these islands have been shaped primarily by events that occurred during the last 12,000 years. Results generally support predictions concerning elevational patterns in species richness and abundance (decreasing with elevation for small fruit bats, increasing with elevation for small non-volant species) and habitat associations of endemic versus non-endemic species (the former restricted to pristine or lightly disturbed habitats, the latter predominant in disturbed habitats). However, some of these patterns appear to break down on small land-bridge islands with relatively depauperate faunas. Most notably, commensal or widespread Asian species are abundant in undisturbed or lightly disturbed habitats when there are few endemic species present. Many of the results have direct implications for wildlife conservation in the Philippines. Patterns of deforestation render lowland species most vulnerable. Habitat associations of species indicate that disturbances to natural habitat have a disproportionately greater negative impact on the unique endemic portions of a local fauna. The depauperate nature of faunas on small land-bridge islands demonstrates that relatively large faunal reserves are required to provide long-term protection for many species. Furthermore, elevational range restrictions or special ecological requirements of some species necessitate reserves that encompass the full range of regional habitat diversity.

Introduction

The Philippine Islands support a diverse mammal fauna of about 170 species, many of which are endemic to the archipelago (Heaney, 1986, 1991a; Heaney et al., 1987). Most studies of Philippine mammals have focused on the faunas of the highlands of the two largest islands, Luzon and Mindanao, principally because early work revealed many endemic species in these areas. As a result of this limited focus, the mammals of most of the smaller Philippine islands remain poorly known. Recent studies on some small and medium-sized islands in the archipelago have yielded a wealth of information on patterns of mammalian distribution (Heaney, 1986; Heaney et al., 1989,

1991; Heaney & Rickart, 1990) and have underscored the importance of such areas both as natural laboratories and as potential faunal reserves.

Unfortunately, this unique fauna is now severely threatened by habitat destruction. Primary forest cover in the Philippines as a whole has been reduced from more than 80% of the total land area near the turn of the century to ca. 8% in 1988 (Myers, 1988), and the destruction continues at an alarming rate. The impact of deforestation on wildlife may be particularly severe on small islands, where population and community structures may be less robust. Forest destruction also poses a very direct threat to human welfare. In addition to the loss of invaluable forest resources, the elimination of natural watershed protection in upland regions greatly increases the likelihood of seasonal flooding. On 5 November 1991, this last possibility became a terrible reality in northern Leyte, where thousands of Filipinos lost their lives in catastrophic floods and landslides associated with a tropical storm. The scope of this disaster was certainly magnified by the extensive logging that has virtually eliminated interior forests throughout most of the region.

In this paper we present the first synoptic lists of mammals from three islands in the central Visayan group: Leyte, the eighth largest island in the Philippine archipelago, and Biliran and Maripipi, two small islands immediately north of Leyte (fig. 1). All three were part of the island of Greater Mindanao during a period of lower sea level in the late Pleistocene, becoming isolated about 10,000 years ago (Heaney, 1986). In relation to present-day Mindanao (with an area of 99,078 km^2), Leyte (7,213 km^2), Biliran (498 km^2), and Maripipi (22 km^2) represent a graded series of sizes, each differing from the next by a similar factor. Each of these islands retains some areas representing the three major types of natural forest vegetation: lowland forest, montane forest, and mossy forest (or dipterocarp, lower montane, and upper montane rain forest; *sensu* Whitmore, 1984).

It is our purpose to assess the taxonomic status and summarize available ecological information for all mammal species known to occur on each island. Because many of these species are poorly known, we provide as much detailed information as is practical. Further analysis of distributional data is presented elsewhere (e.g., Heaney et al., 1989; Heaney & Rickart, 1990; Heaney, 1991a).

History of Investigations

Although there are scattered early distributional records of mammals from Leyte (Hollister, 1912, 1913; Taylor, 1934), the history of comprehensive collecting on these islands is limited. In 1963, D. P. Empesso of Silliman University collected bats from within and around the Cathedral Cave complex near Inopacan, Hindang Municipality, Leyte (specimens in the Royal Ontario Museum). During the same decade, G. L. Alcasid and M. Celestino of the Philippine National Museum and D. S. Rabor of Silliman University made collections in the highlands of northern and central Leyte (specimens in the American Museum of Natural History and the Delaware Museum of Natural History). Most of these localities are mapped and briefly described by Parkes (1973). Only small portions of these collections have been described in the literature (Heaney, 1985a; Musser, 1982a,b; Peterson, 1981; Peterson & Fenton, 1970). Prior to our field studies (1981–1987), no surveys had been conducted on either Biliran or Maripipi. A preliminary listing of non-volant mammal species from all three islands appeared in Heaney (1986); however, this did not include the results from our extensive surveys of 1987.

We have attempted to include information on all specimens now in museums. However, most of the information presented here is based on our own field surveys. Our work on Leyte was conducted along an elevational transect on the west-central portion of the island (figs. 1, 2). A brief reconnaissance trip was made to this region from 23 to 28 May 1984 (voucher specimens in the University of Michigan Museum of Zoology [UMMZ]), but most work took place from 2 March to 13 April 1987 (specimens in the Philippine National Museum [PNM], the Silliman University Museum [SU], the United States National Museum of Natural History [USNM], the Visayas State College of Agriculture [VISCA], and the Western Aus-

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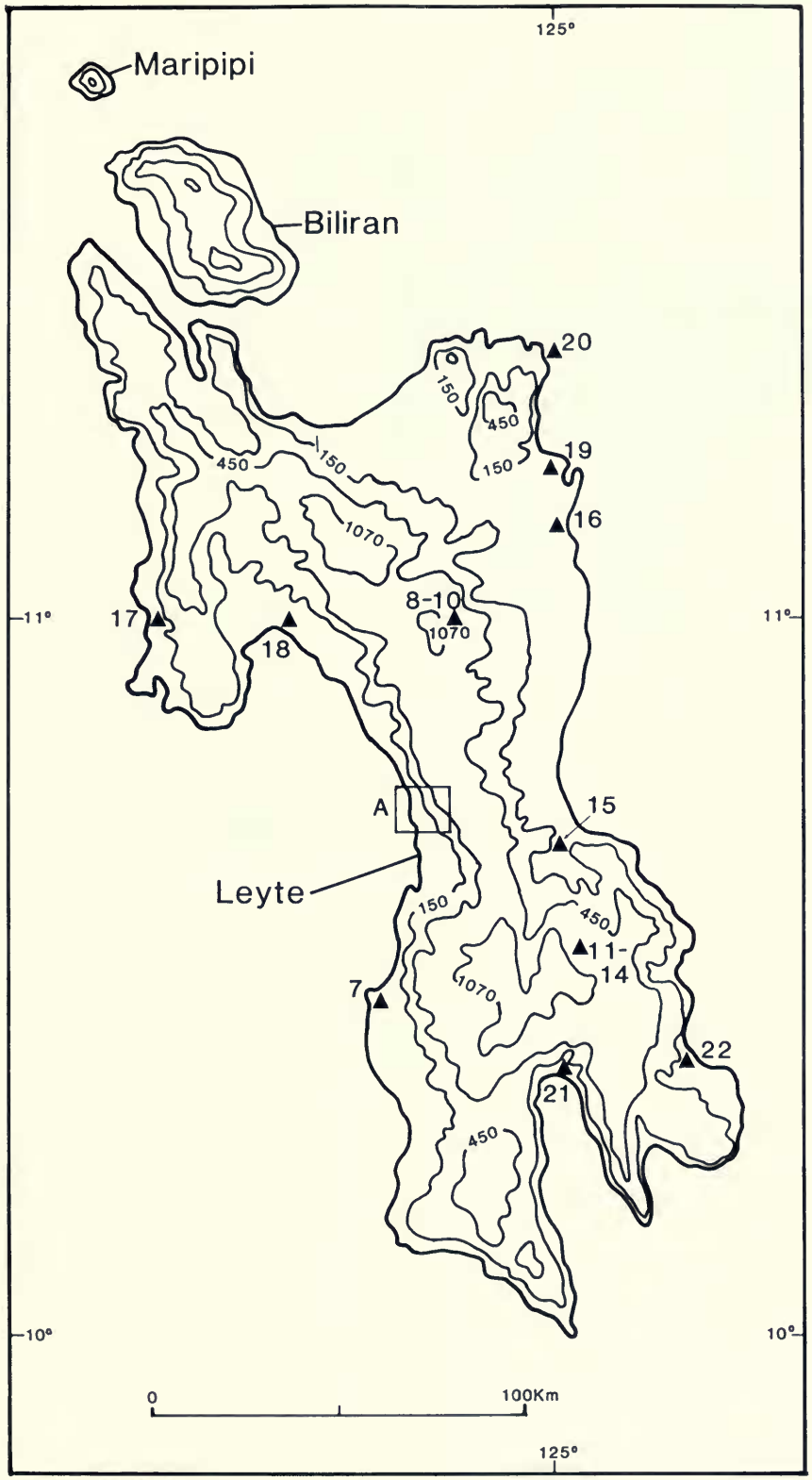
FIG. 1. Map of Leyte Island, showing the relative positions of Biliran and Maripipi islands and the locations of Leyte collecting sites (as enumerated in text). A = site of the elevational transect in the VISCA–Mt. Pangasugan region (sites L1–L6) shown in Figure 2. Contour lines in meters.


125°
Maripipi
Biliran
20
150
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16
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Leyte
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14
7
1070
22
21
450
10°
10°
0
100Km
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tralian Museum [WAM]). In 1984 we initiated work on Biliran with brief surveys of two sites from 27 April to 3 May (specimens in UMMZ). During a second field season from 10 to 28 April 1987, we investigated two sites intensively and three others incidentally (specimens in PNM, SU, and USNM). Field work on Maripipi took place from 4 to 7 July 1981 (specimens in UMMZ), from 4 to 8 May 1984 (specimens in UMMZ), and from 15 to 27 April 1987 (specimens in PNM, SU, and USNM).

Geology

The geological history of the Philippines has been outlined in detail elsewhere (Heaney, 1985b, 1986). Here we provide only a general summary as it applies to the study region.

The Philippine Islands have formed along subduction zones at the margins of lithospheric plates, primarily as a result of anticlinal folding and volcanic activity. Although small amounts of continental crustal material are present on some islands, these lie beneath younger marine deposits. Evidence therefore indicates that the archipelago emerged *de novo* as an oceanic group. The island of Leyte consists primarily of Miocene limestones and marine volcanics, indicating that it probably did not emerge before the Pliocene. There are also several Quaternary volcanoes on Leyte, and much of the island interior is covered by relatively young volcanic material. Likewise, Biliran and Maripipi are entirely covered by volcanic material (Hamilton, 1979; Ollier, 1985; Mitchell et al., 1986).

The periodic advance and recession of continental glaciers during the Pleistocene epoch were accompanied by global changes in sea level. In the Philippine archipelago, the lower sea levels associated with glacial maxima resulted in larger island areas and periods of connection between many present-day islands. With the exception of the Palawan region, however, the Philippines have never had a direct land connection with mainland Asia. During the latest glacial episode, about 18,000 years ago, sea level was approximately 120 m lower than at present (Donn et al., 1962; Bloom, 1983). Leyte, Biliran, and Maripipi, which are now separated from one another by relatively shallow channels (<70 m minimum water depth), were then encompassed within the single large Pleistocene island of Greater Mindanao (Heaney, 1985b, 1991a, b). At that time, Biliran and Maripipi were relatively isolated volcanic highlands in a vast lowland plain extending between present-day Leyte and Samar (fig. 1 in Heaney, 1985b).

Description of Study Areas

Field sites visited by us on each island are listed and described in detail below. Additional Leyte sites visited by previous collectors were taken directly from specimen labels or from the literature. Older sites are identified by the name of a local barrio or principal geographic feature and the encompassing municipality. Although these cannot be located precisely, we have included approximate latitude and longitude coordinates for each. All collecting localities are plotted by site number on the island maps.

Leyte

The island of Leyte (fig. 1) is centered at about 10°50′N, 124°50′E and is located approximately 50 km north of the northern-most point on Mindanao. It is separated from Samar to the northeast by a narrow (2 km) channel. Minimum mid-channel water depth to Mindanao is 80 m, but only ca. 20 m to Samar. The island consists of a low coastal plain of variable width and rugged interior mountain ranges with a maximum elevation of 1350 m. Most of the coastal plain has been cleared for agriculture (principally rice, maize, and sugar cane), but small patches of heavily disturbed secondary forest still existed in some coastal areas in 1987. Much of the forest in the interior has been destroyed or disturbed through extensive logging and upland agriculture. In the area of our field surveys on the west-central portion of the island, undisturbed forest extended down to about 250 m elevation in 1987. At that time we estimated that less than 10% of the island retained primary or moderately disturbed forest. Mean annual precipitation from 1971 to 1986 at Baybay (elev. ca. 5 m) on the western coastal plain was 205 cm, with minimum and maximum monthly means of 7.5 and 24.5 cm in May and December, respectively (Heideman, 1988). Elsewhere in the central Philippines, mid-elevation mountain regions receive up to three times as much rainfall as adjacent lowlands (Manalo, 1956; Heideman & Erickson, 1987). Therefore, mean annual precipitation in the interior highlands on Leyte may exceed 500 cm. Precipitation profiles on Biliran and Maripipi are

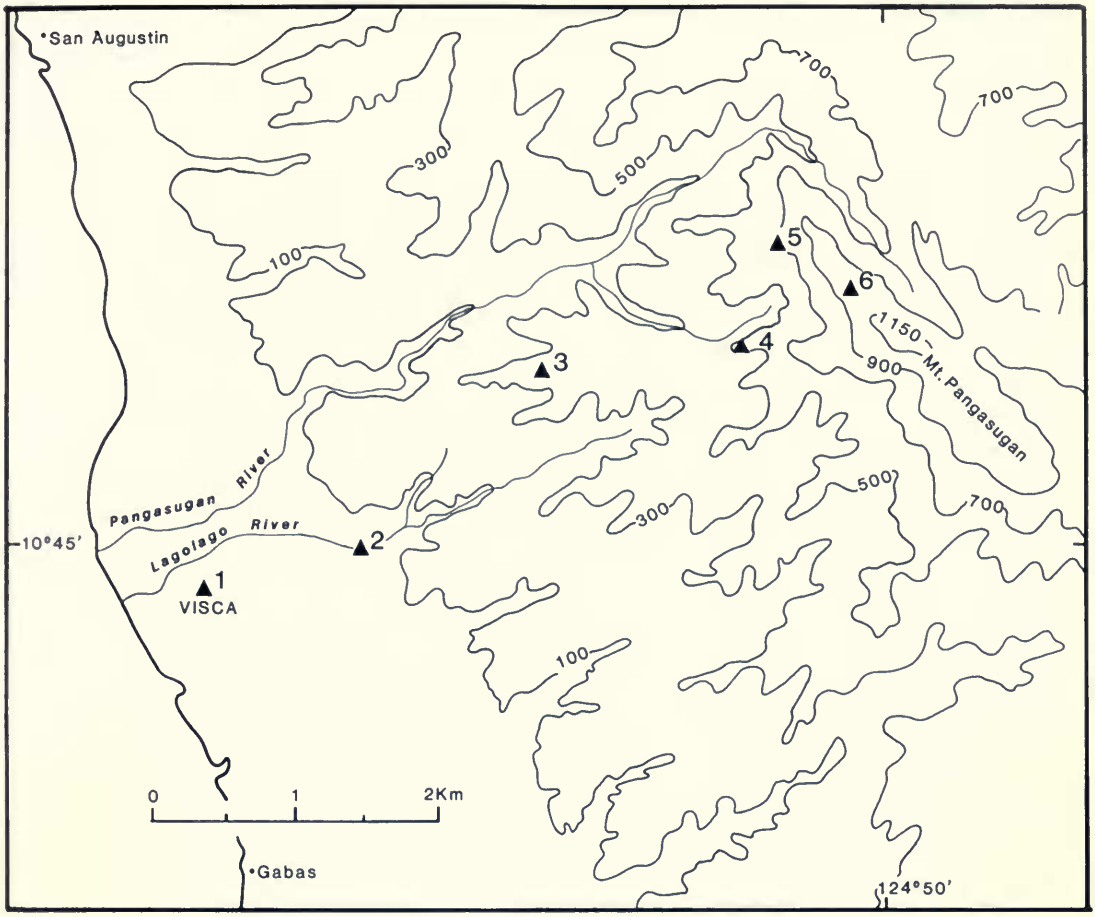

FIG. 2. Map of the elevational transect in the VISCA–Mt. Pangasugan region, Leyte (sites L1–L6). Contour lines in meters.

presumably similar, with some differences due to the effect of smaller island area.

We conducted field work at seven field sites on Leyte. Most of our work was concentrated along an elevational transect on Mt. Pangasugan (summit elev. 1150 m) situated immediately northeast of the campus of the Visayas State College of Agriculture (figs. 1–3). Along this transect, lowland dipterocarp forest extended up to approximately 500 m (fig. 4), followed by mixed lowland dipterocarp–lower montane forest to approximately 800 m (fig. 5), and finally ridgetop mossy forest along the mountain crest from 850 m to the summit (fig. 6). We established four camps in primary forest at 300, 500, 700, and 950 m elevation that served as focal points for intensive survey work (figs. 3–7). Less extensive collecting was done at the base of Mt. Pangasugan in areas of disturbed forest and mixed agricultural land between 50 and 100 m elevation. We also collected bats at the Cathedral Cave complex of limestone caves near Inopacan.

Site L1—*Visayas State College of Agriculture, 7 km N Baybay, Baybay Munic., Leyte Prov., 5–10 m elev., 10°45'N, 124°47'30"E.* We did limited netting in mixed residential and agricultural areas on the college campus, where there was a great variety of fruit trees and flowering plants. We also set a few traps for commensal rodents in campus buildings.

Site L2—*Mt. Pangasugan, 7 km N, 1½ km E Baybay, Baybay Munic., Leyte Prov., 50 m elev., 10°45'N, 124°48'E.* We collected at the base of Mt. Pangasugan immediately above the campus of the Visayas State College of Agriculture. We netted bats at two sites about 400 m apart along a small river in an area of patchwork agricultural land, second growth, and disturbed forest. The first site was surrounded by agricultural land planted with

FIG. 3. Mt. Pangasugan, Leyte (summit elev. 1150 m). View is northeast from the VISCA campus (site L1, ca. 10 m elev.). Site L6 (950 m elev.) was located at the summit of the large subsidiary peak north (left) of the main peak. Photograph taken in March 1987 by E. A. Rickart.

coconut palms (*Cocos nucifera*) and abaca (*Musa textilis*), with scattered remnant forest trees and second growth. The second site was in dense second growth with scattered small patches of abaca, sweet potato, and maize. A few traps were set in forest at the second site (ca. 20 trap-nights). We also hunted in this area.

Site L3—*Mt. Pangasugan, 10 km N, 2 km E Baybay, Baybay Munic., Leyte Prov., 300 m elev., 10°46′N, 124°49′E.* This site was near the lower limit of remaining primary forest on Mt. Pangasugan. It was located on the side of a small valley from ca. 280 m along a small stream to ca. 400 m along an adjacent ridge. Emergent trees (predominantly dipterocarp species) had large buttresses, diameters at breast height (dbh) of 0.8–2.0 m, and heights of 45–55 m. The relatively unbroken canopy ranged from 25 to 40 m high. Large woody vines up to 10 cm in basal diameter were common. Epiphytic ferns and orchids were uncommon, and moss was scarce. An open understory consisted of saplings, small palms, tree ferns (*Cyathea*), erect terrestrial pandans (*Pandanus*), and low ferns. There was a thin covering of leaf litter over rocky volcanic soil.

Site L4—*Mt. Pangasugan, 8½ km N, 2½ km E Baybay, Baybay Munic., Leyte Prov., 500 m elev., 10°45′30″N, 124°49′30″E.* This site was located on a ridge system bounded by steep valleys in undisturbed lowland forest (fig. 4). The canopy was 25–30 m high and broken by numerous tree-falls. Emergent trees with large buttresses had dbh of 0.5–1.5 m and heights up to 40 m. Woody vines were common. Epiphytes, particularly ferns, were common but not abundant. Moss was limited to trunks of large trees and fallen logs. The understory was similar to that at site L3 but more dense. Scattered patches of sedges were also present. There was a moderate layer of leaf litter and humus (up to 20 cm deep) over rocky soil.

Site L5—*Mt. Pangasugan, 10½ km N, 4 km E Baybay, Baybay Munic., Leyte Prov., 700 m elev., 10°46′N, 124°49′30″E.* This site was located along a narrow ridge bounded by cliffs and steep slopes. Vegetation was transitional lowland/montane forest and included some mossy forest elements (fig.

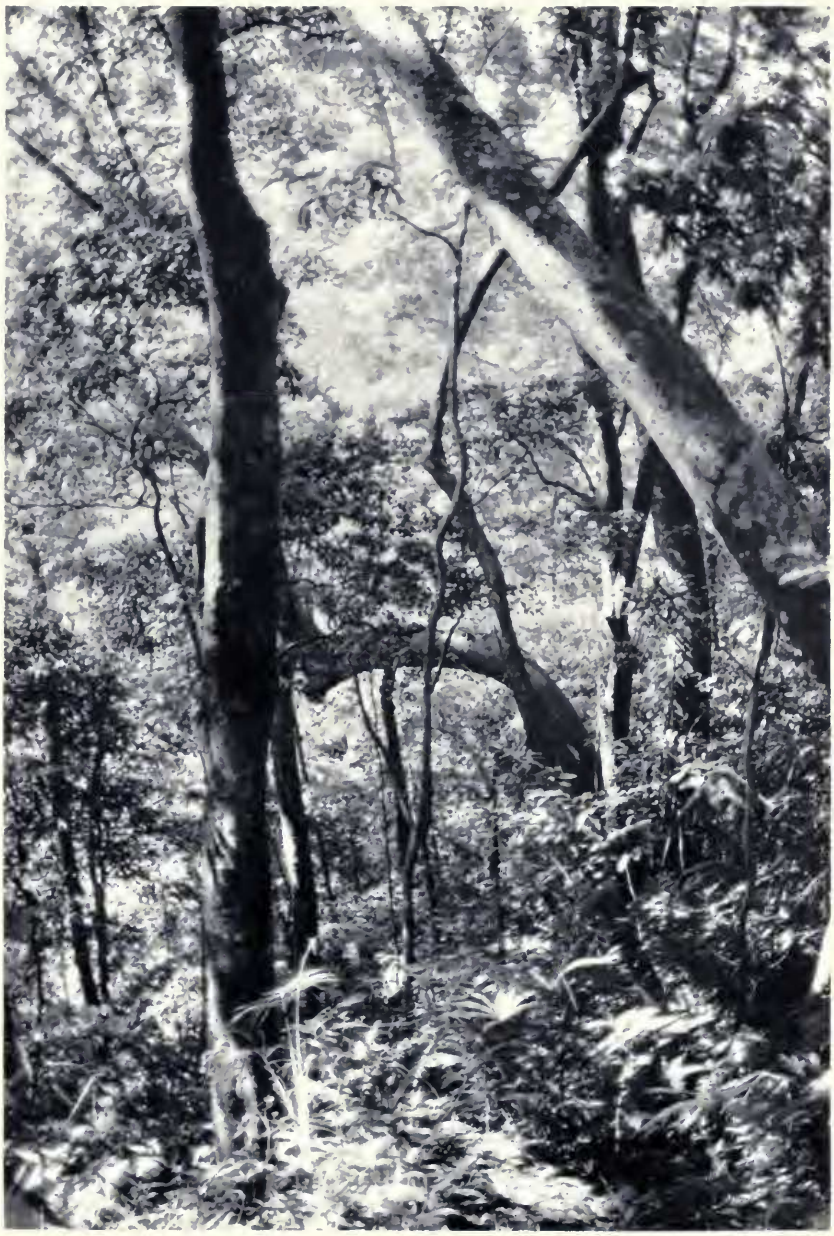

FIG. 4. Lowland dipterocarp forest at ca. 550 m elevation on Mt. Pangasugan, Leyte (near site L4). *Rattus everetti* was the most common small mammal trapped in this habitat, followed by *Apomys littoralis* and *Bullimus bagobus*. The fruit bats *Ptenochirus minor, P. jagori,* and *Rousettus amplexicaudatus* were common, as was the microchiropteran *Rhinolophus inops*. Photograph taken in March 1987 by P. D. Heideman.

5). The broken canopy was at 15–20 m. Emergent trees with little or no buttressing had dbh of up to 1 m and heights up to 30 m. Dipterocarps were uncommon, and an arborescent gymnosperm was present. No trees had leaves with serrated edges. Woody vines and rattan (*Calamus*) were common, and climbing pandans (*Freycinetia*) were present. Epiphytes were common, especially moss, orchids, and ferns. Pitcher plants (*Nepenthes*) were rare. Understory and ground cover were dense, consisting of the same general elements as at lower sites with the addition of sedges and low viny pan-

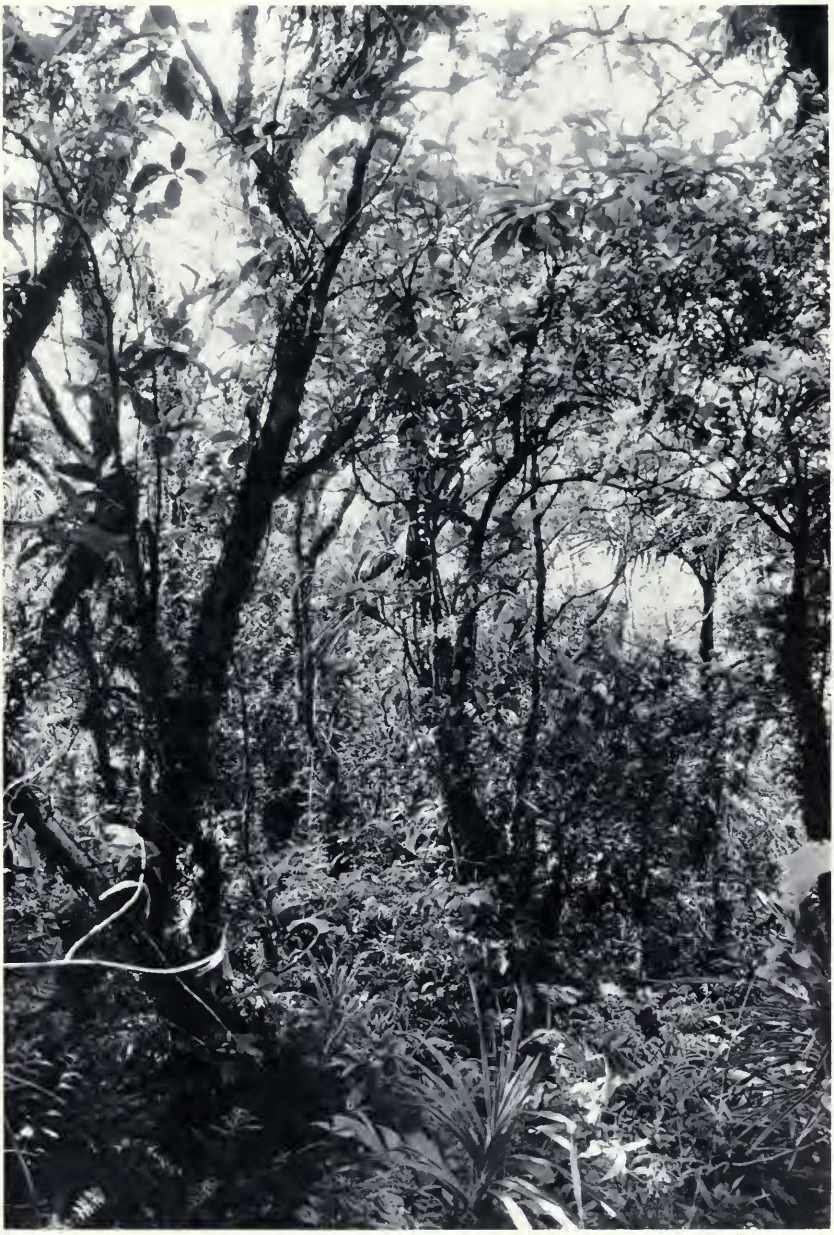

FIG. 5. Transitional lowland–montane forest at ca. 700 m elevation on Mt. Pangasugan, Leyte (near site L5). *Batomys salomonseni* was the most common species trapped here, followed by *Rattus everetti* and *Apomys littoralis. Ptenochirus minor* was the most abundant bat, followed by *Harpyionycteris whiteheadi, Haplonycteris fischeri,* and *Rhinolophus inops.* Photograph taken in March 1987 by P. D. Heideman.

dans. Leaf litter and humus were thick, often in excess of 0.5 m.

Site L6—*Mt. Pangasugan, 10 km N, 4½ km E Baybay, Baybay Munic., Leyte Prov., 950 m elev., 10°47′N, 124°50′E.* This site was located on a high, narrow ridge along the summit crest of Mt. Pangasugan (fig. 6). The ridge varied in width from 5 to 20 m, with narrow points bounded by steep slopes or sheer cliffs. Vegetation was ridgetop mossy forest characterized by the predominance of trees in the families Fagaceae and Ericaceae and the absence of dipterocarps. The open canopy was 5–

FIG. 6. Ridgetop mossy forest at 930 m elevation on Mt. Pangasugan, Leyte (near site L6). *Batomys salomonseni*, *Apomys littoralis*, and *Crocidura beatus* were most abundant in this habitat. *Ptenochirus minor* and *Rhinolophus inops* were the only bat species that were relatively common at this elevation. Photograph taken in March 1987 by P. D. Heideman.

12 m high. The largest trees had dbh of 10–30 cm and were not buttressed. Climbing pandans were abundant, as were epiphytic pitcher plants and orchids. Moss was abundant on nearly all surfaces. The ground was densely covered by viny pandans, moss, sedges, and other herbaceous plants. Leaf litter and humus were very thick, exceeding 0.5 m in many places.

Site L7—*Cathedral Cave area, 4 km S, 1 km E Inopacan, Hindang Munic., Leyte Prov., 60 m elev., 10°28'N, 124°45'E.* We surveyed caves in 1984 and 1987 that lie along a limestone cliff face located about 4 km south of Inopacan. We investigated one large cave and a few of the many small caves at this site. Vegetation uphill from the caves was heavily disturbed secondary forest. Areas downslope were predominantly agricultural land with scattered small patches of second growth. This is the same area in which D. Empesso collected in 1963. Judging from the specimens that he obtained (in the Royal Ontario Museum [ROM]), he collected both within the caves and in surrounding forest and agricultural areas. Undoubtedly, local forests were much more extensive and less disturbed at that time.

The largest cave at this locality, locally known as Cathedral Cave, had a main entrance at the center of a large concavity in the limestone cliff. Several shallow solution pits were located along the face of the concavity outside the cave entrance. The cave was about 100 m deep with two primary rooms. One room was about 40 m wide and 30 m long, varied from 10 to 30 m high, and had many small grottoes on the sides. The second room was larger (ca. 50 m by 60 m) and higher (ca. 40 m), contained few side passages, and was well lit through a large opening in the ceiling.

A second site, located about 100 m downhill from the entrance to Cathedral Cave, consisted of cavities under large pieces of limestone that had separated from the cliff. The resultant system of narrow passageways probably extended along much of the cliff face.

In 1984 we visited two additional caves located about ½ km south of Cathedral Cave along the same hillside. One cave was moderately large, with

FIG. 7. View northeast from the crest of Mt. Pangasugan (near site L6), showing extent of forest between ca. 600 and 1100 m elevation. Photograph taken in March 1987 by P. D. Heideman.

a length of 25–30 m, a width of 10–20 m, and an average height of 5–6 m; the ceiling was irregular, with bats clustering in deep solution holes. The other cave was about 100 m away and was 25 m long, 5 m wide, and 1–2.5 m high.

ADDITIONAL LEYTE COLLECTING LOCALITIES—**Site L8**—*Barrio Buri, Mt. Lobi Range, Burauen Munic., Leyte Prov., 600–850 m elev., ca. 11°00′N, 124°50′E.*

Site L9—*Barrio Tambis, Mt. Lobi Range, Burauen Munic., Leyte Prov., 150–700 m elev., ca. 11°00′N, 124°50′E.* The areas around Barrio Buri and Barrio Tambis in the Mt. Lobi region (sites L8 and L9) were visited by D. S. Rabor in 1964 (specimens in the Delaware Museum of Natural History [DMNH]). At that time, areas below 500 m elevation were a mixture of cultivated fields, cleared hills, *parang* (mixed second growth and grassland), and secondary forest. Areas of primary dipterocarp forest were still extant above 500 m elevation, with transitional montane forest at the highest elevations (Parkes, 1973).

Site L10—*Barrio Patok, Mt. Lobi Range, Dagami Munic., Leyte Prov., ca. 11°01′N, 124°50′E.* This was the primary collection area of G. L. Alcasid and M. Celestino in 1961 (specimens in the American Museum of Natural History [AMNH]). At that time, the vicinity of Patok was agricultural (abaca and coconuts). Forests persisted above 300 m elevation but were broken in many places up to 600 m elevation by recently logged clearings (Parkes, 1973).

Site L11—*Bulog Pk., Mt. Kabalanti-an, Mahaplag Munic., Leyte Prov., 1500–2000 ft (450–600 m) elev., ca. 10°36′N, 125°00′E.*

Site L12—*Barrio Paniniklan, Mt. Kabalanti-an, Mahaplag Munic., Leyte Prov., 800–1000 ft (250–300 m) elev., ca. 10°36′N, 125°00′E.*

Site L13—*Barrio Santa Cruz, Mahaplag Munic., Leyte Prov., ca. 10°36′N, 125°00′E.* Localities in the vicinity of Mt. Kabalanti-an in the Municipality of Mahaplag (sites L11–L13) were visited by D. S. Rabor in 1964 (specimens in DMNH and the University of the Philippines [UPLB]). At that time, areas at lower elevations were predominantly croplands (corn and rice). Higher elevations were covered with mixtures of primary and secondary forest (Parkes, 1973).

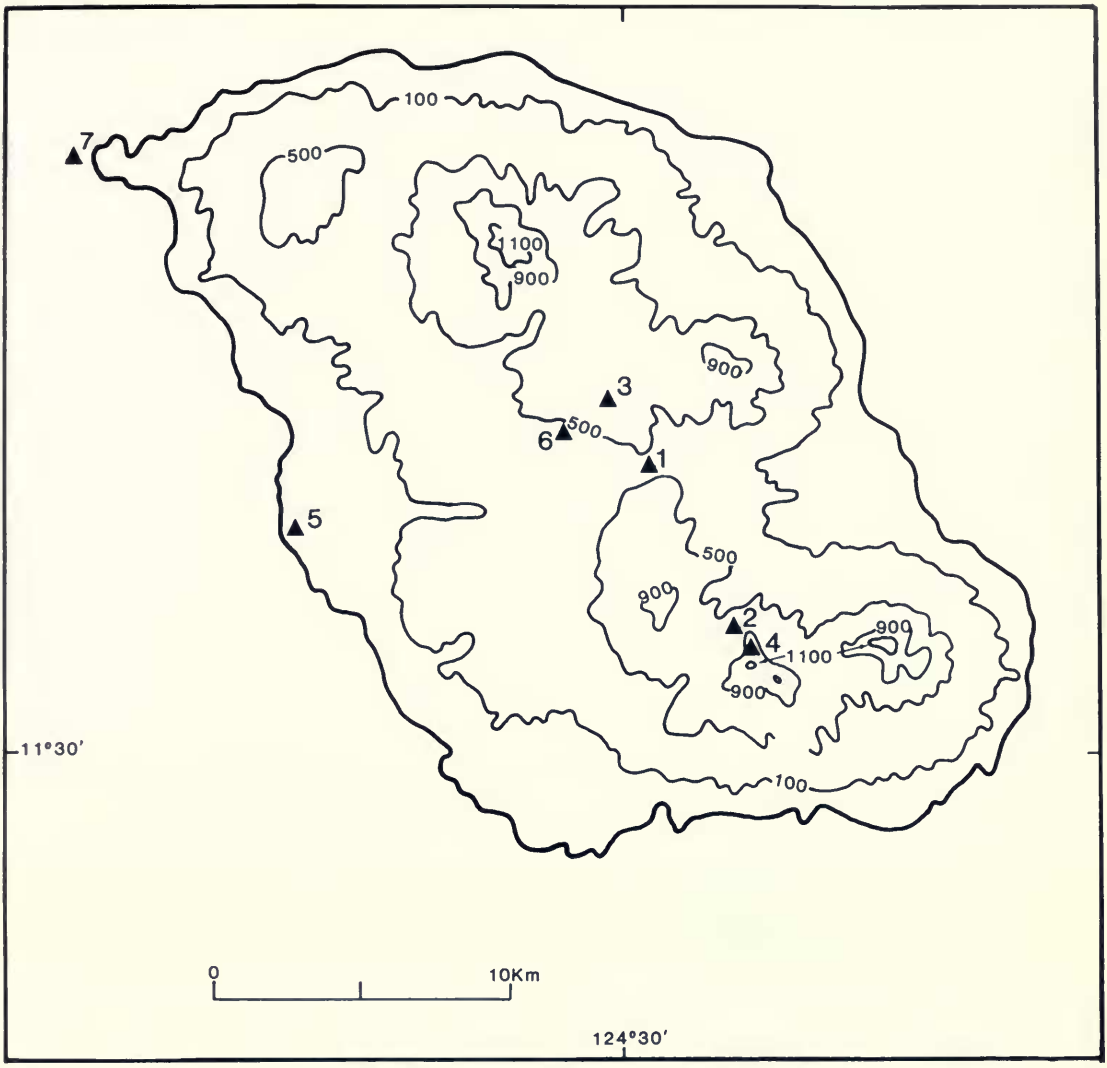

FIG. 8. Map of Biliran Island, showing locations of collecting sites (as enumerated in text). Contour lines in meters.

Site L14—*Paril Cave, Mahaplag Munic., Leyte Prov., ca. 10°36'N, 125°00'E.* An undescribed locality visited by Alcasid and Celestino in 1961 (specimens in AMNH).

Site L15—*Barrio Balinsasayao, Abuyog Munic., Leyte Prov., 10°40'N, 124°57'E.* An undescribed locality visited by Alcasid and Celestino in 1961 (specimens in AMNH).

Site L16—*Palo, Leyte Prov., 11°10'N, 125°00'E.* An undescribed locality, probably urban, for series of *Scotophilus kuhlii* and *Rattus rattus* (specimens in the Field Museum of Natural History [FMNH]).

Site L17—*Palompon, Leyte Prov., 11°03'N, 124°23'E.* An undescribed site, probably urban, for a series of *Scotophilus* (specimens in the ROM; not seen).

Site L18—*Vicinity of Ormoc, Leyte Prov., 11°01'N, 124°37'E.* Undescribed localities in this vicinity are cited for *Cynopterus brachyotis* (specimens in ROM) and *Cervus mariannus* (specimen at VISCA).

Site L19—*Vicinity of Tacloban, Leyte Prov., 11°14'N, 125°00'E.* An undescribed locality for a specimen of *Cynocephalus volans* (specimen in USNM).

Site L20—*Small island in channel between Leyte and Samar, ca. 11°25'N, 124°55'E.* An undescribed locality, presumably an island roost, where

FIG. 9. View of the southern slope of Mt. Konduko, Biliran (summit elev. 1045 m) and the adjacent valley near site B1 (located at the extreme left center of the photograph). Site B3 was located in a saddle on the north slope of Mt. Konduko below the small peak just visible behind the western (left) flank of the mountain. Lower elevations support a mosaic of agricultural land, second growth, forest plantation, and small patches of remnant forest. Large forest tracts are restricted to slopes above 800 m elevation. Photograph taken in April 1987 by L. R. Heaney.

Steere (1890) collected a series of *Acerodon jubatus* (specimens in FMNH and USNM).

Site L21—*Consolacion, Southern Leyte Prov., 10°23'N, 125°00'E.* An undescribed locality for *Tarsius* cited by Taylor (1934).

Site L22—*Vicinity of Hinunangan, Southern Leyte Prov., ca. 10°24'N, 125°11'E.* An undescribed locality for *Cervus mariannus* (specimen at VISCA).

Biliran

This volcanic island (fig. 8), centered at 11°35'N, 124°30'E, is separated from northwestern Leyte by a sea channel 1 km wide. A broad coastal plain around much of the island perimeter grades into low hills and an interior that is dominated by five small ridge systems. The highest interior peaks range in elevation from 1000 to 1340 m. As of 1987, most of the interior land below 500 m elevation had been cleared for agriculture (primarily the production of coconut and abaca hemp), with small remnant patches of heavily disturbed forest restricted to the steepest ridges. Between 500 and 800 m, gentler slopes had been cleared and the remaining forest had been extensively logged (figs. 9, 10). Disturbance due to logging was less extensive above 800 m, but large trees had been selectively cut from all but the steepest slopes and least accessible areas; the small areas of montane forest, where trees are naturally small, were undisturbed. We estimated that less than 50 km^2 (less than 10% of the total island area) remained covered by primary or lightly disturbed forest. Most of the timber removed in recent years had been cut illegally by loggers using handsaws, with shaped timbers dragged out to roads by water buffalos (fig. 11). Most logging had occurred after 1980, when a bridge between Biliran and Leyte was completed. Logging continued at a rapid rate during our 1984 and 1987 field seasons. Local residents told us that

FIG. 10. Eastern slope of Mt. Konduko, Biliran, at ca. 700 m elevation. View is toward the summit from a point along the cleared ridge seen at the right edge of Figure 9. The foreground and middleground were recently cleared and burned and are dominated by *cogon* grass (*Imperata*) and scrubby vegetation with scattered young coconut palms. Higher slopes (above 800 m) remain forested. Photograph taken in April 1987 by L. R. Heaney.

the principal market was a single business in Naval, which provided trucks for transporting lumber from roadsides.

Site B1—*2½ km N, 11 km E Naval town, Caibiran Munic., 450 m elev., 11°35'N, 124°30'E.* In 1987 we netted (8 net-nights) and trapped (61 trap-nights) in a Bureau of Forest Development reforestation station at 400–450 m. A 20-ha forest plantation and an adjacent 20-ha patch of heavily logged remnant primary forest formed an island of trees separated from primary forest by about 0.5 km of agricultural land and sparse second growth. The plantation was dominated by *ipil-ipil* (*Leucaena*) and other fast-growing trees with a volunteer understory of native trees and herbs. Adjacent agricultural land included rice fields, coconut groves, and fruit tree orchards. The patch of remnant forest covered a hillside from 400 to 500 m elevation. The canopy was discontinuous and the understory dense with small trees, shrubs, and vines. The few remaining large trees (dbh > 15 cm; height to 30 m) were hollow or otherwise damaged.

Site B2—*3½ km S, 5½ km W Caibiran town, Caibiran Munic., 700 m elev., 11°32'N, 124°32'E.* In 1984 we netted (ca. 36 net-nights) and trapped (ca. 212 trap-nights) in mixed partially logged and primary lowland forest. Although the forest was in the process of being logged, trees of up to 50 cm dbh were still common (fig. 11). The canopy was at 15–20 m and broken by abundant small clearings where large trees had been felled. A brief inspection in 1987 showed the area to be covered by abaca and dense second growth beneath a highly discontinuous canopy of trees up to 20 cm dbh.

Site B3—*Mt. Konduko, 5 km N, 10 km E Naval town, Naval Munic., 850 m elev., 11°36'30"N, 124°29'E.* In 1987 we netted (74 net-nights) and trapped (451 trap-nights) in montane forest centered on a saddle along a ridge at 800–950 m on the north side of Mt. Konduko (summit elev. 1045 m). The forest on the saddle received moisture-laden air, producing some characteristics of higher elevation mossy forest. The canopy was 12–15 m in height with numerous gaps due to tree-falls.

FIG. 11. Area of recent illegal logging in lowland forest at 700 m elevation on Biliran (near site B2). *Apomys littoralis, Batomys salomonseni, Rattus everetti, R. exulans,* and *R. rattus* were trapped in this area. *Haplonycteris fischeri, Ptenochirus minor, P. jagori,* and *Macroglossus minimus* were relatively common. Photograph taken in April 1984 by P. D. Heideman.

Most large trees were stunted and broken due to wind damage. Ferns and orchids were common epiphytes, and moss was common on the trees. There was a moderately dense understory of tree ferns, saplings, small palms, erect terrestrial pandans, viny pandans, and wild banana. Soil was rocky, with scattered deep pockets of humus and some leaf litter. Trees below the saddle were larger (20 m canopy, emergents to 25 m, dbh up to 50 cm) and supported similar but denser epiphyte loads. Canopy height declined to 3 m on nearby higher ridges; epiphytes and moss were uncommon in such places. Trees were absent from the crests of the highest knolls where viny pandans, sedges, and low-growing shrubs predominated.

Site B4—*4½ km S, 5 km W Caibiran town, Caibiran Munic., 920 m elev., 11°32'N, 124°32'E.* In 1984 we conducted limited trapping (91 trap-nights) and netting (4–8 net-nights) in disturbed ridgetop montane forest above site B2.

Site B5—*Naval town, 5 m elev., 11°34'N, 124°24'E.* In 1984 and 1987 we made incidental collections of bats in and around residential buildings in the town of Naval.

BILIRAN CAVE LOCALITIES—The caves that we found were all in igneous rock, either cracks in cliff faces or gaps between large boulders in breakdown piles below cliffs. All were small with narrow and mostly shallow passages. We saw no limestone on the island and thus doubt that there are large caves.

Site B6—*4 km N, 9½ km E Naval town, Naval Munic., 500 m elev., 11°36'N, 124°29'E.* In 1987 we collected a series of *Emballonura alecto* from a small rockfall cave located in a boulder field at the base of a steep granite cliff on the southwest flank of Mt. Konduko. The cave had a single large chamber measuring ca. 1 m by 3 m. Surrounding vegetation was brushy second growth.

Site B7—*Caves on Tincansan Island, Kawayan Munic., 11°40'30"N, 124°19'30"E.* In 1981 we collected bats at two sea caves on Tincansan Island, a small (ca. ⅛ km²) islet located about 300 m off the northwest coast of Biliran. One consisted of a single concavity about 3 m wide, 4½ m high, and

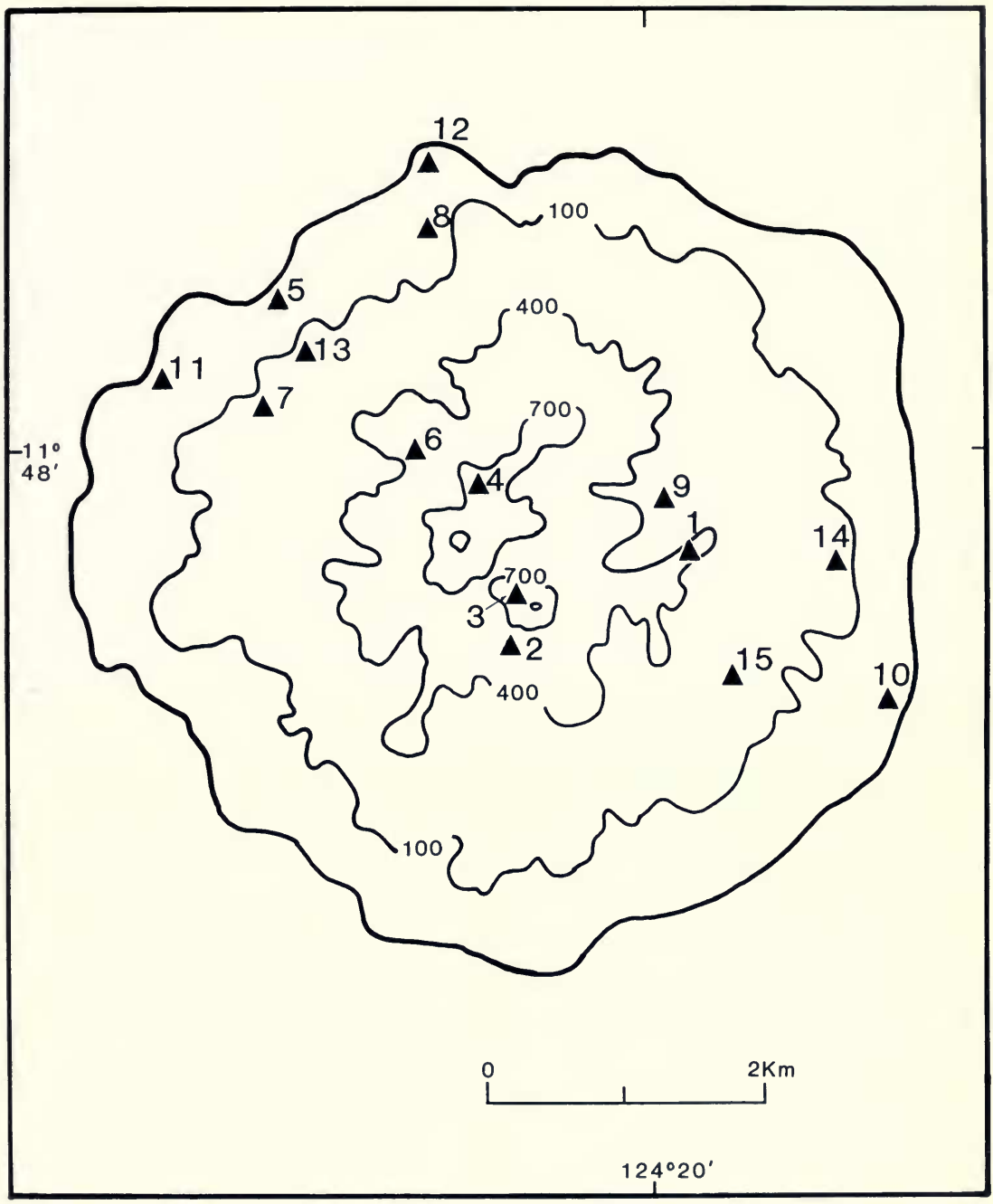

FIG. 12. Map of Maripipi Island, showing locations of collecting sites (as enumerated in text). Contour lines in meters.

5 m deep. The second cave was larger, consisting of a single passageway 6 m wide, 4 m high, and ca. 20 m deep. This second cave was exposed to surf and the floor was covered with deep water.

Maripipi

This small, roughly circular volcanic island (fig. 12) is centered at 11°47′N, 124°20′E immediately

FIG. 13. The island of Maripipi (maximum elev. 924 m), view from the southeast. Photograph taken in April 1987 by P. D. Heideman.

north of Biliran. It is separated from Biliran by a channel about 9 km wide with a minimum mid-channel depth of 60 m. The island rises steeply from the sea to form a single major mountain with two high peaks (fig. 13). The larger peak is formed by three interconnected ridges that rise to 924 m; the subsidiary peak is 806 m high. The coastal bench is only about 1 km wide and has been completely cleared and planted, primarily with coconut palms. In 1987 the lowest primary forest was at 200 m on the steepest slopes. Most of the gentler slopes had been cleared to an elevation of about 500 m. We estimated that an area of 3–4 km^2 (15–20% of the total island area) was covered by primary or lightly disturbed forest in 1987.

Site M1—*1 km N, 1½ km W Maripipi town, 300–400 m elev., 11°47′30″N, 124°20′E.* In 1981 we netted (10 net-nights) and trapped (100 trap-nights) in a steep valley along forest edge and in disturbed lowland forest (fig. 14). The extant forest was restricted to steep slopes, where only the largest trees had been removed. Eighty-eight trap-nights were in this forest, most along the banks of a dry, rocky streambed. Soil was thin and rocky. Twelve trap-nights were in a nearby camote patch. Nets were placed in the forest and on the forest edge.

Site M2—*½ km N, 2½ km W Maripipi town, 600–700 m elev., 11°47′N, 124°19′E.* In 1984 we netted (15 net-nights), trapped (137 trap-nights), and hunted in secondary forest and old second growth on the upper slopes of the 800 m peak. The forest had been burned more than 30 years prior to our collecting. Some flat land had been cultivated at about that time. The low canopy (5–10 m) included tree ferns and was broken by frequent gaps. Trees had dbh of less than 20 cm. The understory was rich with ferns and herbaceous plants. Vines were abundant, but moss and other epiphytes were rare.

Site M3—*½ km N, 2½ km W Maripipi town, 800 m elev., 11°47′N, 124°19′E.* In 1984 we did limited collecting (127 trap-nights, 6 net-nights) in a small area of ridgetop mossy forest above site M2 (fig. 15). The habitat was similar to that of site M4.

FIG. 14. Clearing in disturbed lowland forest at ca. 300 m on Maripipi (site M1). *Crocidura beatus* and *Rattus rattus* were trapped in this area. *Cynopterus brachyotis* was the most common fruit bat. Photograph taken in July 1981 by P. D. Heideman.

Site M4—*2 km N, 3 km W Maripipi town, 600–800 m elev., 11°48′N, 124°19′E.* In 1987 we netted (49 net-nights) and trapped (611 trap-nights) in primary and lightly disturbed ridgetop montane forest from 600 to 800 m on the ridge system of the highest peak on the island. The forest had a broken canopy of 6–8 m on the ridge crests and a few meters higher on ridge sides. Trees of the families Lauraceae and Ericaceae (dbh up to 50 cm) were predominant. An arborescent gymnosperm was also present, whereas dipterocarps were absent. Most trees had moss on their trunks, some of which was up to 8 cm thick. Orchids and other epiphytes were abundant, as were rattans, viny pandans (*Freycinetia*), and climbing bamboo (*Schizostachyum*). Ground cover was dense with abundant ferns, sedges, and pandans. Soil was thin and rocky. In some flat, protected areas, emergent trees up to 25 m with dbh of 100 cm were present (although the canopy was generally no higher). In these places ground cover was slightly less dense and epiphytes were generally confined to emergent trees. At 600 m elevation, a small partial clearing created by removal of understory growth was replanted with cacao (*Theobroma*) seedlings.

Site M5—*Vicinity of Viga, sea level to 200 m elev., 11°48′30″N, 124°18′E.* In 1987 we conducted a small amount of netting (5 net-nights) in and around the town of Viga in agricultural areas adjacent to second growth and remnant forest. We also set a few traps for commensal species in buildings (11 trap-nights).

Site M6—*Ca. 2 km N, 3½ km W Maripipi town, 500 m elev., 11°48′N, 124°19′E.* In 1987 we obtained a commensal mouse (*Mus*) that had been hand-caught at this site (a farm building in a clearing at the edge of primary forest).

Site M7—*Ca. 2 km N, 4 km W Maripipi town, 100–200 m elev., 11°48′N, 124°18′E.* In 1987 we received some specimens that had been caught in this area of disturbed lowland forest and coconut plantation.

Site M8—*3½ km N, 3½ km W Maripipi town, 50 m elev., 11°49′N, 124°19′E.* In 1987 we ob-

FIG. 15. Ridgetop mossy forest at 800 m elevation on Maripipi (site M3). *Crocidura beatus* and *Rattus everetti* were trapped at this site, and the fruit bats *Harpyionycteris whiteheadi, Pteropus pumilus,* and *Macroglossus minimus* were netted here. Photograph taken in April 1984 by P. D. Heideman.

served and collected *Pteropus hypomelanus* at roosts in two 35 m remnant forest trees in a grove of 15–20 m coconut palms near the coast. The roost trees were separated by 300 m and were at least 500 m from the nearest disturbed forest.

Site M9—*1½ km N, 1½ km W Maripipi town, 200–400 m elev., 11°47′30″N, 124°20′E.* In 1984 and 1987 we observed and collected *Acerodon jubatus* in an area of mixed remnant forest and coconut plantation between 200 and 400 m elevation. Several separate roost trees occurred in an area of ca. 30 ha: a 35 m remnant emergent surrounded by 15 m coconut palms, a 20 m *Ficus* located among smaller trees at the edge of a cliff ca. 500 m from the first roost, and a 1 ha cluster of about 10 emergent trees on the edge of the same cliff 300 m from the *Ficus.*

Site M10—*Vicinity of Maripipi town, near sea level, 11°47′N, 124°21′E.* In 1981 we obtained a few specimens from buildings in the town of Maripipi and from nearby forest.

MARIPIPI CAVE LOCALITIES—All of the caves that we found were in igneous rock. These consisted of cracks in large rocks or cliff faces, or of gaps beneath large rocks in the breakdown piles at the bases of cliffs. We found nine such caves from the edge of the sea to 800 m elevation but found bats only in caves between sea level and 200 m. All these caves were small, with narrow passageways, and often with multiple entrances. None had negotiable passages deeper than 10 m. A complete circuit of the island's coast revealed no limestone; therefore, we doubt there are any large caves.

Site M11—*Ca. 3 km N, 5 km W Maripipi town, 50 m elev., 11°48′N, 124°18′E.* In 1987 we purchased some *Emballonura alecto* that had been collected by local boys from a small rockfall cave at this approximate locality.

Site M12—*4 km N, 3½ km W Maripipi town, 10 m elev., 11°49′N, 124°19′E.* In 1987 we collected *Emballonura alecto, Taphozous melanopogon,* and *Hipposideros ater* from a rockfall cave complex in an agricultural area on the northern coast of the island. The cave was located among boulders at the base of a 30 m cliff near sea level. Multiple openings led to several large chambers up to 10 m deep that were connected by narrow, twisting passageways.

Site M13—*3 km N, 4 km W Maripipi town, 100–200 m elev., 11°48′N, 124°18′30″E.* In 1987

we obtained a series of *Emballonura alecto* from a small rockfall cave at this site. The cave was among boulders at the base of a cliff in an area of mixed agricultural land, second growth, and remnant forest.

Site M14—*Ca. 1 km N, ½ km W Maripipi town, ca. 200 m elev., 11°47'30"N, 124°20'30"E.* In 1981 we collected a series of *Emballonura alecto* at this site, located in primary forest approximately 1 km east of site M1. The cave consisted of a single chamber approximately 5 m long and 3 m high, with one main entrance and several smaller openings.

Site M15—*Ca. ½ km N, 1½ km W Maripipi town, 200 m elev., 11°47'N, 124°20'E.* In 1984 we obtained a small series of *Emballonura alecto* that had been collected from an undescribed rockfall cave at this approximate location.

Methods

Our field studies were conducted using procedures that evolved over time. The primary purpose of surveys in 1981 and 1984 was to ascertain species diversity on the separate islands. The 1987 surveys had the additional aim of documenting elevational patterns in species richness and abundance. These later surveys involved greater standardization of field methods, particularly with respect to baits used in small mammal trapping, placement of traps and mist nets, number of nights that traps and nets were run, and total effort (number of trap- and net-nights) at a given locality (Heaney et al., 1989).

Murid rodents and shrews were caught in trap lines containing a mixture of Victor rat traps (ca. 65%), National live traps (25%), and Sherman live traps (10%) spaced 5–15 m apart with one trap per station. Most traps were set on the ground (90%), most often along runways, near holes, or within root tangles. Other traps were set aboveground on fallen trees, horizontal branches, or large vines. Separate trap lines of 20–50 traps typically were operated for 4–6 days; a few were run longer to increase captures of trap-shy species. Traps were baited in the late afternoon with fresh-fried coconut and peanut butter (occasionally with addition of small amounts of other ingredients such as essential oils and banana) and checked and rebaited near dawn. Occasionally traps were also checked in the early afternoon and evening. Alternative trapping methods (e.g., snares, drift fences, pitfalls) that may be more effective in capturing certain species were used on a few occasions. We did not use live earthworms as bait, although they subsequently have proven to be very effective in capturing some species that are marginally attracted to standard baits (Rickart et al., 1991).

Bats were caught in mist nets set on ridgetops, across established trails and streams, or at the edge of clearings in forests, and among fruit trees in agricultural areas. Most nets were 2.6 m high and 12 m long and had 36 mm mesh size, but smaller nets were used occasionally. In all years our mist-netting efforts included data on the number of individuals of each species caught per net each night. In 1987 netting was more standardized with respect to the number of net-nights per site (generally more than 20) and number of nights each net was operated (three to six nights). On most nights, mist nets were tended continuously during the primary activity peak in the early evening (ca. 1800–2000 hours), although some were tended longer or checked only twice per evening. Thereafter, nets remained open all night and were checked at dawn.

On each island we used additional means to census large mammals and species that are otherwise difficult to trap or net. These efforts involved direct observation, hunting (air rifle, .22 caliber rifle, or .410 caliber shotgun), limited purchase of old trophy specimens from local residents, and interviews with local residents. Trapping and netting sites were well separated to minimize depletion of local populations and to ensure that sampling at one site did not influence sampling at another. Some animals were released after positive identification; others were preserved as voucher specimens for taxonomic and anatomical studies. Each of our field crews consisted of at least one of the authors and one previously trained field technician (usually two of each), two or more local assistants, and often collaborators from other institutions. On Leyte, two crews usually worked different sites simultaneously.

To provide comparative data on geographic variation and as an aid to identification, we have attempted to examine and measure as many specimens as possible. These are enumerated by locality and institution under Specimens Examined in individual species accounts. Cranial measurements were made by Heaney to the nearest 0.1 mm using dial or digital calipers. Limits of cranial measurements are defined by DeBlase and Martin (1974). External measurements were taken from specimen labels or collectors' field notes. Specimens referred to are housed in the American Museum of Natural History (AMNH), the Delaware

TABLE 1. The number of insectivores and rodents trapped at principal sites on Leyte, Biliran, and Maripipi islands. The number of captures per 100 trap-nights are given in parentheses.

	Leyte				Biliran				Maripipi		
Species	L3 (300 m)	L4 (500 m)	L5 (700 m)	L6 (950 m)	B1 (450 m)	B2 (700 m)	B3 (850 m)	B4 (920 m)	M1 (400 m)	M2 (700 m)	M4 (740 m)
Crocidura beatus	0	2 (0.24)	0*	6 (0.41)	0	0	1 (0.22)	0	1 (1)	0	0
Apomys littoralis	2 (0.22)	7 (0.85)	6 (0.53)	16 (1.10)	0	4 (1.89)	4 (0.89)	8 (8.80)	0	0	0
Batomys salomonseni	0	1 (0.12)	14 (1.24)	21 (1.45)	0	2 (0.94)	1 (0.22)	0	0	0	0
Bullimus bagobus	6 (0.65)	2 (0.24)	0	0	0	0	0	0	0	0	5 (0.82)
Rattus everetti	9 (0.97)	11 (1.34)	8 (0.71)	4 (0.28)	0	4 (1.89)	11 (2.44)	1 (1.10)	0	1 (0.73)	8 (1.31)
Rattus exulans†	0	0	0	0	0	2 (0.94)	0	0	0	0	0
Rattus rattus†	0	0	0	0	4 (6.56)	3 (1.42)	4 (0.89)	3 (3.30)	2 (2)	5 (3.65)	5 (0.82)
Total captures	17	23	28	47	4	15	21	12	3	6	18
Total trap-nights	930	819	1125	1451	61	212	451	91	100	137	611
Total mammals per 100 trap-nights	1.83	2.81	2.49	3.24	6.56	7.08	4.66	13.19	3	4.38	2.94
Number of species	3	5	3 (+ 1)*	4	1	5	5	3	2	2	3

* Inferred from presence at lower and higher elevations.
† Introduced commensal species.

Museum of Natural History (DMNH), the Field Museum of Natural History (FMNH), Philippine National Museum (PNM), the Royal Ontario Museum (ROM), the Silliman University Museum (SU), the United States National Museum of Natural History (USNM), the University of Michigan, Museum of Zoology (UMMZ), the University of the Philippines at Los Baños (UPLB), Visayas State College of Agriculture (VISCA), and the Western Australian Museum (WAM). Voucher specimens collected by us are deposited at PNM, UMMZ, USNM, VISCA, and WAM.

Taxa are presented alphabetically within families. Unless noted otherwise, species names follow Honacki et al. (1982). Subspecies names are given where they have been used consistently and unambiguously in recent taxonomic literature. For each species, we summarize the known distributional limits (based on Heaney et al., 1987, unless stated otherwise) and report known records of occurrence on the three islands. Specific collecting localities are referred to by site number. We provide tables of external and cranial measurements and discuss discernable patterns of geographic

TABLE 2. Means (± SD) and ranges of selected measurements of adult *Crocidura beatus* from Leyte, Biliran, and Maripipi islands.

Locality	Sex	N	Condylo-basal length	Braincase width	Inter-orbital width	Rostral length	Rostral width	Post-palatal depth	Post-palatal length	Occipital condyle to glenoid fossa
Leyte	♂	2	21.6 (21.6–21.7)	9.6 (9.3–9.8)	4.7 (4.6–4.8)	8.6	2.6 (2.5–2.7)	3.9	9.6 (9.4–9.8)	8.6 (8.5–8.6)
	♀	4	21.1±0.38 (20.6–21.5)	9.5±0.19 (9.4–9.8)	4.7±0.31 (4.3–5.0)	8.4±0.20 (8.3–8.7)	2.8±0.24 (2.5–3.0)	3.9±0.17 (3.7–4.1)	9.4±0.13 (9.3–9.6)	8.3±0.13 (8.1–8.4)
Biliran	♀	1	—	9.5	—	—	—	3.7	9.8	8.7
Maripipi	♀	2	21.0 (20.6–21.5)	9.4 (9.2–9.5)	4.8 (4.8–4.9)	8.5	2.6 (2.6–2.7)	3.7	9.4 (9.3–9.7)	8.2 (8.0–8.5)

Note: Measurements other than weight are in millimeters.

variation within the study region. Finally, we summarize available information on ecology and behavior of species, relying primarily on our field notes.

Accounts of Species

Order **Insectivora**
Family **Soricidae**—Shrews

Crocidura beatus Miller, 1910

Prior to our work, this species of white-toothed shrew was reported from Mindanao only (Heaney et al., 1987; Heaney & Ruedi, in press). On Mt. Pangasugan, Leyte, shrews were present in primary lowland forest at 500 m (site L4) and common in mossy forest at 950 m elevation (site L6). A single specimen from Biliran was trapped in primary montane forest at 850 m elevation (site B3). On Maripipi, one specimen was caught near a dry streambed in disturbed lowland forest at 385 m (site M1) and another was taken in ridgetop mossy forest at 800 m elevation (site M3). The species has a broad elevational range but is most common in high-elevation forest (table 1). All of the specimens we collected were trapped on the ground within leaf litter, in runways, or along steep, moss-covered embankments. Three specimens were captured during full daylight. A female captured on 20 April on Biliran was carrying a single embryo (crown–rump length = 3 mm). Cranial and external measurements of adult specimens from the three islands are listed in Table 2.

SPECIMENS EXAMINED—Total 13. LEYTE: Leyte Prov.: site L4 (2 USNM); site L6 (6 USNM); site L9 (2 DMNH). BILIRAN: site B3 (1 USNM). MARIPIPI: site M1 (1 UMMZ); site M4 (1 USNM).

Suncus murinus occultidens (Hollister, 1913)

The widespread Oriental house shrew occurs throughout the Philippines, primarily in the lowlands near human habitations. The two known specimens from Leyte were hand-caught soon after sunrise near buildings on the campus of the Visayas State College of Agriculture (site L1). None were taken on Biliran or Maripipi, but we did not make extensive efforts to obtain commensal species on either island.

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L1 (1 UMMZ, 1 USNM).

Order **Dermoptera**
Family **Cynocephalidae**—"Flying Lemurs"

Cynocephalus volans (Linnaeus, 1758)

The kagwang, or Philippine "flying lemur," is restricted to the Mindanao faunal region; previous records are from Basilan, Bohol, Dinagat, Leyte, Mindanao, Samar, and Siargao. Thomas (1911) reported the species to be common on Leyte but did not list specific localities. In the Mt. Pangasugan region, our field party obtained two specimens from local hunters. Both were captured in an area of secondary forest adjacent to a small coconut plantation at about 50 m elevation (site L2). In the same area, we sighted individual animals on consecutive evenings shortly after dusk as they glided between coconut palms. Another specimen was taken on Mt. Pangasugan in primary forest at 500 m elevation (site L4). Several other individuals were sighted at sites below 500 m in

TABLE 2. *Extended.*

First incisor to third molar	Fourth premolar to third molar	Labial width at second molars	Palatal width at third molars	Total length	Tail length	Hindfoot	Weight (g)
9.5 (9.4–9.6)	5.4 (5.3–5.4)	6.4	2.4 (2.3–2.4)	145	59 (53–65)	16	11.2 (11.0–11.5)
9.2±0.24 (9.0–9.5)	5.2±0.12 (5.1–5.4)	6.4±0.05 (6.3–6.4)	2.6±0.10 (2.5–2.7)	151±13.6 (135–163)	62±11.1 (52–75)	15±1.2 (14–16)	11±1.4 (10–12)
–	5.3	6.3	2.3	144	56	16	11
9.3 (9.1–9.5)	5.4 (5.2–5.5)	6.5 (6.4–6.6)	2.7 (2.6–2.8)	150 (146–153)	68 (68–69)	16 (15–17)	9.0 (8.5–9.5)

TABLE 3. Selected measurements of adult *Cynocephalus volans* from Leyte and Biliran islands.

	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth	Rostral length	Orbital length	Post-orbital length
Leyte*	♂	1	—	—	—	—	—	—	—	—
	♀	1	—	—	—	—	—	—	—	—
Biliran†	♂	1	66.0	41.8	16.7	15.0	30.2	25.3	24.2	25.7

Note: Measurements other than weight are in millimeters.
* No cranial measurements.
† No external measurements.

both primary and secondary forest. A specimen from the vicinity of Tacloban (site L19) was obtained from Bureau of Forest Development personnel. This animal, an unweaned juvenile male, was caught with an adult female on 18 March. On Biliran, an adult male (scrotal testes 17 × 14 mm) was shot at 450 m elevation in an isolated 20 ha patch of remnant lowland primary forest approximately ½ km from larger areas of forest (site B1). No kagwang were taken on Maripipi, but local residents reported that they were common. Shortly after dawn on 7 July 1981, Heideman saw two kagwang gliding between trees in partially cleared lowland forest at 300 m elevation (site M1). According to local farmers and hunters on Leyte, the species is common in both disturbed and primary forest habitats in lowland areas below 500 m elevation, is active both night and day, and typically feeds on young leaves and fruit of a variety of tree species. Specimens from Leyte and Biliran (table 3) fall within the range of size variation seen in series from Dinagat, Siargao, and Mindanao (Heaney & Rabor, 1982).

SPECIMENS EXAMINED—Total 10. LEYTE: Leyte

TABLE 4. Means (± SD) and ranges of selected measurements of adult fruit bats (*Acerodon* and *Cynopterus*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth	Rostral length	Orbital length	C to last M
Acerodon jubatus										
Leyte	♂	3	80.7 (79.9–82.2)	43.8 (42.9–45.1)	12.5 (12.0–13.1)	9.1 (8.9–9.3)	24.4 (23.9–25.0)	29.1 (27.9–30.2)	30.6 (29.8–31.6)	32.3 (31.7–33.0)
	♀	8	80.7±1.41 (79.1–83.1)	42.3±0.58 (41.2–43.7)	12.4±0.77 (11.6–13.6)	9.3±0.44 (8.8–10.1)	24.4±0.95 (23.2–25.7)	29.1±1.40 (27.5–31.2)	30.7±0.50 (30.0–31.6)	32.6±0.77 (30.9–33.3)
Maripipi	♂	3	81.0 (78.3–85.9)	44.8 (41.3–48.3)	11.9 (11.1–13.1)	8.8 (8.3–9.4)	25.0 (24.0–26.3)	28.8 (26.9–31.7)	30.5 (29.3–32.3)	33.2 (31.8–35.7)
	♀	4	78.1±1.70 (76.7–80.3)	42.1±1.37 (40.1–43.2)	11.8±0.19 (11.7–12.1)	9.0±0.64 (8.4–9.9)	24.1±0.57 (23.3–24.5)	27.9±0.85 (27.2–29.1)	29.8±0.86 (29.1–30.9)	31.3±0.81 (30.2–31.9)
Cynopterus brachyotis										
Leyte	♂	6	28.2±0.54 (27.4–28.8)	18.6±0.50 (17.9–19.2)	6.0±0.38 (5.4–6.5)	6.2±0.53 (5.5–6.8)	12.0±0.22 (11.6–12.2)	9.0±0.26 (8.6–9.3)	11.8±0.26 (11.4–12.1)	9.4±0.35 (9.0–9.9)
	♀	7	27.8±0.51 (27.1–28.4)	18.4±0.44 (18.0–19.1)	6.0±0.31 (5.5–6.4)	6.3±0.29 (5.9–6.6)	11.8±0.49 (11.0–12.6)	8.5±0.35 (7.9–8.9)	12.1±0.39 (11.6–12.7)	9.4±0.15 (9.2–9.6)
Biliran	♂	4	28.4±0.34 (28.1–28.8)	19.1±0.38 (18.7–19.4)	6.1±0.06 (6.0–6.1)	6.3±0.32 (6.0–6.7)	12.0±0.21 (11.7–12.2)	9.1±0.30 (8.8–9.5)	12.1±0.49 (11.5–12.7)	9.3±0.18 (9.1–9.5)
	♀	10	27.3±0.59 (26.5–28.4)	18.3±0.43 (17.6–19.1)	6.1±0.50 (5.5–7.0)	6.3±0.48 (5.7–7.4)	11.7±0.37 (11.0–12.1)	8.7±0.44 (8.0–9.5)	11.7±0.37 (11.2–12.3)	9.1±0.26 (8.7–9.7)
Maripipi	♂	7	27.4±0.82 (26.2–28.2)	18.1±0.35 (17.6–18.7)	6.1±0.25 (5.6–6.3)	6.5±0.54 (5.3–7.0)	11.9±0.31 (11.5–12.3)	8.7±0.24 (8.4–9.1)	11.8±0.46 (11.0–12.4)	9.3±0.21 (9.0–9.6)
	♀	8	27.2±0.79 (26.4–28.5)	18.4±0.36 (17.7–18.9)	6.1±0.23 (5.6–6.4)	6.3±0.29 (5.9–6.8)	11.9±0.31 (11.4–12.4)	8.7±0.42 (8.1–9.2)	11.8±0.33 (11.1–12.3)	9.1±0.22 (8.7–9.4)

Note: Measurements other than weight are in millimeters.
* Measured from dry skins.

TABLE 3. *Extended.*

C to last M	Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Weight (g)
–	–	–	–	–	275	81	29	1,360
–	–	–	–	645	260	86	29	1,160
31.6	20.7	14.2	32.1	–	–	–	–	–

Prov.: site L2 (2 USNM); site L4 (1 UMMZ); site L10 (5 AMNH); site L19 (1 USNM). BILIRAN: site B1 (1 USNM).

Order **Chiroptera**
Family **Pteropodidae**—Fruit Bats

Acerodon jubatus (Eschscholtz, 1831)

The golden-capped flying fox is a Philippine endemic that is found throughout the country with the exception of the Palawan region. Günther (1879) reported this species from southern Leyte. Specimens taken by Steere (1890) on a small island midway in the channel between Leyte and Samar (site L20) were named *Pteropus aurinuchalis* (Elliot, 1896), but they are not now recognized as distinct. We did not encounter this species during our field work on Leyte, nor did we obtain any specimens on Biliran. We received reports of flying fox roosts on Biliran but did not locate any. On several occasions, however, we saw giant fruit bats flying at dusk over our campsites on Biliran or

TABLE 4. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
23.4 (22.9–23.8)	16.4 (16.1–16.9)	47.0 (46.6–47.4)	–	0	65*	28* (28–29)	203* (198–208)	–
23.6±0.68 (22.6–24.7)	16.4±0.33 (15.8–16.8)	45.6±1.59 (43.2–47.5)	–	0	66±2.9* (65–70)	27±2.5* (23–30)	192±5.8* (184–202)	–
23.7 (22.6–24.8)	16.2 (14.4–17.9)	46.2 (44.0–49.9)	298 (280–319)	0	66 (60–73)	39 (37–41)	193 (187–203)	954 (750–1,140)
22.8±0.70 (22.1–23.8)	16.6±0.85 (15.9–17.7)	44.5±1.11 (43.1–45.8)	286±10.1 (273–296)	0	65±5.2 (60–70)	36±0.6 (36–37)	192±5.1 (186–196)	948±170 (720–1,100)
6.6±0.23 (6.4–6.9)	6.2±0.29 (5.7–6.5)	14.1±0.35 (13.6–14.5)	101±8.1 (96–117)	9±3.3 (6–15)	15±0.8 (14–16)	18±0.4 (18–19)	64±1.5 (62–66)	30±2.3 (26–32)
6.6±0.08 (6.5–6.7)	6.2±0.28 (5.8–6.6)	14.0±0.46 (13.4–14.6)	101±3.3 (96–105)	8±2.3 (4–10)	15±1.0 (14–16)	18±0.8 (17–19)	64±2.1 (61–67)	30±1.7 (28–32)
6.5±0.14 (6.4–6.7)	6.3±0.14 (6.1–6.4)	14.5±0.50 (14.1–15.2)	100±5.1 (93–104)	8±1.2 (7–9)	16±1.3 (15–18)	18±0.6 (18–19)	64±2.1 (61–66)	32±2.1 (30–34)
6.5±0.23 (6.1–6.9)	6.1±0.22 (5.7–6.3)	13.8±0.38 (13.4–14.6)	99±5.1 (88–105)	8±0.6 (7–9)	16±1.7 (13–18)	18±0.8 (17–19)	64±2.1 (61–66)	33±2.7 (28–38)
6.5±0.21 (6.3–6.9)	6.0±0.34 (5.5–6.5)	14.0±0.48 (13.2–14.6)	97±2.9 (93–101)	8±1.9 (5–10)	14±2.0 (10–16)	17±1.6 (14–19)	62±2.2 (59–65)	31±1.8 (28–33)
6.5±0.15 (6.2–6.7)	6.2±0.27 (5.8–6.6)	13.9±0.45 (13.2–14.6)	97±3.8 (91–103)	6±2.3 (3–10)	14±0.6 (13–15)	17±0.5 (17–18)	62±1.1 (61–64)	32±2.8 (29–38)

TABLE 5. The number of small fruit bats (Pteropodidae) netted at principal sites on Leyte, Biliran, and Maripipi islands. The number of captures per net-night are given in parentheses.

	Leyte					Biliran				Maripipi		
Species	L2 (50 m)	L3 (300 m)	L4 (500 m)	L5 (700 m)	L6 (950 m)	B1 (450 m)	B2 (700 m)	B3 (850 m)	B4 (920 m)	M1 (400 m)	M2 (700 m)	M4 (740 m)
Cynopterus brachyotis	39 (1.56)	2 (0.03)	4 (0.05)	3 (0.02)	0	17 (2.13)	6 (0.24)	6 (0.08)	0	14 (1.40)	11 (0.73)	32 (0.65)
Eonycteris robusta	0	0	0	0	0	0	1 (0.04)	0	0	0	1 (0.07)	0
Eonycteris spelaea	28 (1.12)	0*	2 (0.03)	0	0	2 (0.25)	1 (0.04)	0	0	3 (0.30)	0	0
Haplonycteris fischeri	0	2 (0.03)	1 (0.01)	11 (0.09)	3 (0.09)	1 (0.13)	26 (1.04)	43 (0.58)	3	0	0	0
Harpyionycteris whiteheadi	0	1 (0.01)	6 (0.08)	12 (0.10)	0	0	0	0†	1	0†	0†	2 (0.04)
Macroglossus minimus	20 (0.80)	4 (0.05)	3 (0.04)	4 (0.03)	1 (0.03)	5 (0.63)	10 (0.40)	9 (0.12)	4	4 (0.40)	1 (0.07)	15 (0.31)
Ptenochirus jagori	40 (1.60)	14 (0.18)	18 (0.23)	2 (0.02)	0	16 (2.00)	27 (1.08)	2 (0.03)	3	10 (1.00)	6 (0.40)	12 (0.24)
Ptenochirus minor	12 (0.48)	23 (0.30)	21 (0.27)	84 (0.68)	11 (0.33)	0	24 (0.96)	51 (0.69)	10	0	0	0
Rousettus amplexicaudatus	13 (0.52)	0*	10 (0.13)	3 (0.02)	0	63 (7.80)	0	0	0	1 (0.10)	11 (0.73)	2 (0.04)
Total captures	152	46	65	119	15	104	95	111	21	32	30	63
Total net-nights	25	77	79	123	33	8	25	74	4–8	10	15	49
Bats/net-night	6.08	0.60	0.82	0.97	0.45	13.0	3.80	1.50	—	3.20	2.00	1.29
Number of species	6	6 (+ 2)*	8	7	3	6	8	6	5	6	6	5

* Inferred from presence at lower and higher elevations.
† Known to be present (from vocalizations) but not captured.

flying toward Biliran from Maripipi. Given the proximity of large colonies on Maripipi, we believe these bats were *Acerodon jubatus*. On Maripipi, we collected 10 individuals of this species from roost trees in an area of mixed remnant forest and coconut plantation (site M9). In 1987 each of about 12 roost trees at this site had groups of 50–150 bats (apparently all *A. jubatus*); we estimated a total colony size of ca. 1,000. Individuals appeared to be evenly spaced within the tree crowns. When one bat approached another, the usual result was an aggressive display involving vocal threats and "boxing" with closed wings (striking with the wrists). Within a short time, one bat usually retreated or flew from the tree, often returning to another position within the same tree. Many bats hung with their wings partly spread, occasionally flapping them gently, and sometimes licking the wing membranes and panting. This behavior probably prevented overheating. Two adult females collected in May 1984 and another taken on 26 April 1987 held large embryos (crown–rump lengths = 75–106 mm; 99–148 g). In April 1987 the abdomens of most females were swollen with near-term embryos, but no females were carrying nursing young. A young female taken on this date (believed to be a yearling on the basis of external and cranial measurements) was not pregnant. These observations suggest that *A. jubatus* on Maripipi produce their single yearly young in late May and June, and that females may not reproduce until 2 years of age. Leyte and Maripipi specimens exhibit slight sexual dimorphism, with males averaging slightly larger in most cranial and external measurements (table 4).

SPECIMENS EXAMINED—Total 21. LEYTE: Leyte Prov.: site L20 (2 FMNH, 9 USNM). MARIPIPI: site M9 (6 UMMZ, 4 USNM).

Cynopterus brachyotis luzoniensis Peters, 1862

The short-nosed fruit bat is common throughout the Philippines and is widely distributed in

Southeast Asia (Koopman, 1989). It typically is associated with forest clearings and other disturbed habitats (Heaney et al., 1989; Heideman & Heaney, 1989). In the Mt. Pangasugan region on Leyte, this was the most common pteropodid species taken in disturbed secondary forest at 50 m (site L2) and in mixed agricultural and residential areas below 50 m elevation (site L1). It was uncommon in primary lowland and montane forest between 300 and 700 m elevation (sites L3–L5) and absent from ridgetop mossy forest (site L6; table 5). Similarly, on Biliran it was abundant in disturbed lowland forest and second growth reforested areas (site B1) but rarely encountered in primary forest (site B3; table 5). On Maripipi, in contrast to the situation on all other islands where we have worked (Heaney et al., 1989, 1991), *C. brachyotis* was abundant in all habitats and was the most frequently captured bat species in primary mossy forest at 750 m (site M4; table 5). On Maripipi, we found one individual roosting in a 3 m shrub amid moderately dense undergrowth in primary forest at 800 m elevation. Adult females taken from late March through early July contained single embryos. Cranial and external measurements (table 4) fall within ranges reported for specimens from various locations throughout the Philippines (Heaney & Rabor, 1982; Heaney, 1984; Heaney et al., 1991). Males are slightly larger than females in some cranial dimensions. Leyte specimens have a karyotype of 2n = 34, FN = 58, that is indistinguishable from those of specimens from elsewhere in the species' geographic range (Rickart et al., 1989a). Kitchener and Maharadatunkamsi (1991) have suggested that *C. b. luzoniensis* be recognized as a separate species, but we recommend further investigation of geographic variation before this is accepted.

Specimens Examined—Total 134. LEYTE: Leyte Prov.: site L1 (10 USNM); site L2 (2 PNM, 33 USNM); site L3 (2 USNM); site L4 (2 UMMZ, 4 USNM); site L5 (3 USNM). BILIRAN: site B1 (2 PNM, 15 USNM); site B2 (8 UMMZ); site B3 (6 USNM). MARIPIPI: site M1 (14 UMMZ); site M2 (4 UMMZ); site M4 (2 PNM, 27 USNM).

Other Records—LEYTE: site L7 (ROM); site L18 (ROM).

Eonycteris robusta Miller, 1913

This nectar bat is a widespread Philippine endemic with records from Catanduanes, Luzon, Mindanao, Negros, and Siargao Islands (Heaney & Rabor, 1982; Heideman & Heaney, 1989; Heaney et al., 1991). Some authors have considered it to be a subspecies of *E. major* (Honacki et al., 1982; Koopman, 1989). *Eonycteris robusta* is not common and may rely on primary forest habitat. We captured none during the course of our field work on Leyte, but specimens were taken at Tambis (site L9), Paniniklan (site L12), and Santa Cruz (L13) in Leyte Province during the 1960s. On Biliran in April 1984, we netted a 68 g adult female carrying a 13 g neonate in partially logged primary forest at 700 m (site B2). On Maripipi, an adult male was netted at 600 m on a cleared ridgetop above old second growth forest (site M2). Measurements of specimens from all three islands are larger than those of series from Luzon and Catanduanes (Heaney & Rabor, 1982; Heaney et al., 1991). In the large series from Leyte, males are substantially larger than females (table 6).

Specimens Examined—Total 20. LEYTE: Leyte Prov.: L9 (1 DMNH); L12 (1 DMNH); L13 (15 DMNH). BILIRAN: site B2 (2 UMMZ). MARIPIPI: site M2 (1 UMMZ).

Eonycteris spelaea glandifera Lawrence, 1939

The cave nectar bat occurs from India to Timor and is common throughout the Philippines. On Leyte in 1987, we found large numbers of this species within solution cavities in the ceiling of Cathedral Cave (site L7). Several separate groups contained between 200 and 500 individuals, with a total population probably in excess of 2,000 individuals. The species has been heavily persecuted at this site: a large pile of dried skins and charred bones representing several hundred individuals was found at the cave entrance, and we found evidence of torches and fires within the cave. Nectar bats were common in mixed second growth and agricultural areas at the base of Mt. Pangasugan but rare in primary forest at 500 m on the mountain (sites L2 and L4; table 5). On Biliran, two specimens were netted in mixed agricultural land and replanted forest at 400 m (site B1), and one was taken in partially logged primary forest at 700 m (site B2). On Maripipi, three specimens were captured at the edge of disturbed forest at 300 m (site M1). On Negros, *Eonycteris spelaea* is associated with forest clearings and other disturbed habitats (Heideman & Heaney, 1989). Based on our rela-

TABLE 6. Means (± SD) and ranges of selected measurements of adult fruit bats (*Eonycteris* and *Haplonycteris*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth	Rostral length	Orbital length	C to last M
Eonycteris robusta										
Leyte	♂	6	36.2±2.11 (32.7–37.9)	23.1±0.58 (22.5–23.8)	7.4±0.59 (6.6–8.1)	7.7±0.61 (7.4–8.6)	14.7±0.66 (13.6–15.3)	13.8±1.23 (11.9–14.7)	12.8±0.62 (12.1–13.6)	13.1±0.96 (11.8–14.0)
	♀	11	33.2±1.04 (32.1–35.0)	20.0±0.74 (19.1–21.0)	7.1±0.27 (6.6–7.6)	8.2±0.51 (7.1–8.9)	13.5±0.36 (13.0–14.1)	12.6±0.95 (11.6–14.1)	12.4±0.61 (11.7–13.9)	12.1±0.40 (11.6–12.9)
Biliran	♀	1	35.9	20.8	7.1	7.9	14.2	13.9	13.1	13.4
Maripipi	♂	1	35.4	22.0	6.9	7.2	14.1	13.3	12.7	12.8
Eonycteris spelaea										
Leyte	♂	6	34.3±0.76 (33.2–35.2)	21.7±1.11 (19.7–23.0)	6.9±0.18 (6.6–7.1)	7.7±0.37 (7.2–8.3)	14.4±0.61 (13.6–15.3)	12.9±0.35 (12.3–13.4)	12.5±0.35 (12.1–13.1)	12.1±0.56 (11.6–13.2)
	♀	8	33.3±0.75 (32.1–34.3)	20.0±0.43 (19.3–20.7)	6.7±0.12 (6.5–6.9)	7.5±0.42 (7.0–8.2)	13.4±0.36 (12.8–14.0)	12.2±0.54 (11.2–12.7)	12.3±0.29 (11.9–12.7)	12.1±0.56 (11.3–13.3)
Biliran	♂	1	33.7	22.6	7.0	7.9	14.9	12.6	12.8	11.9
Maripipi	♀	2	33.2 (33.0–33.3)	19.4 (19.1–19.8)	6.6	7.5 (7.4–7.6)	13.0 (12.8–13.1)	12.4 (11.6–13.3)	12.6 (12.5–12.6)	12.2 (12.0–12.3)
Haplonycteris fischeri										
Leyte	♂	8	23.9±0.64 (23.1–24.8)	16.5±0.40 (15.8–17.1)	6.3±0.29 (5.8–6.8)	6.0±0.28 (5.7–6.6)	11.0±0.26 (10.7–11.4)	7.8±0.55 (7.1–8.5)	10.1±0.22 (9.8–10.4)	8.6±0.29 (8.2–8.9)
	♀	8	23.9±0.60 (22.8–24.8)	16.5±0.42 (15.9–17.3)	6.0±0.42 (5.3–6.7)	5.9±0.14 (5.7–6.1)	10.8±0.18 (10.6–11.0)	7.7±0.34 (7.2–8.1)	10.1±0.33 (9.8–10.6)	8.4±0.33 (7.7–8.6)
Biliran	♂	8	24.3±0.58 (23.3–24.8)	16.4±0.51 (15.7–17.3)	6.3±0.14 (6.0–6.4)	6.2±0.29 (5.5–6.4)	10.9±0.40 (10.4–11.6)	7.8±0.26 (7.5–8.2)	10.3±0.48 (9.7–10.9)	8.5±0.31 (8.1–8.9)
	♀	10	24.3±0.73 (22.9–24.8)	16.4±0.42 (15.7–17.3)	6.2±0.31 (5.4–6.4)	6.1±0.33 (5.6–6.7)	10.8±0.31 (10.4–11.5)	7.7±0.43 (6.8–8.4)	10.3±0.39 (9.8–11.0)	8.4±0.31 (7.8–9.1)

Note: Measurements other than weight are in millimeters.

tive netting success, the species is most common in lowland agricultural areas and is rare or absent in primary forest (table 5; Heaney et al., 1989). It is most abundant in the vicinity of limestone caves that serve as primary roost sites. Pregnant females containing single embryos (crown–rump lengths = 4–33 mm) were taken during April. Lactating females with dependent young were taken in March at Cathedral Cave on Leyte. Cranial measurements of males are slightly larger than those of females (table 6). Measurements fall within the ranges of specimens from Catanduanes, Luzon, and Siargao (Heaney & Rabor, 1982; Heaney et al., 1991). Karyotypes of specimens from Leyte are 2n = 36, FN = 66, and are indistinguishable from those reported for specimens taken elsewhere in the species' distribution (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 80. LEYTE: Leyte Prov.: site L2 (1 SU, 6 USNM); site L4 (2 USNM); site L7 (37 DMNH, 2 PNM, 17 UMMZ, 9 USNM). BILIRAN: site B1 (2 PNM); site B2 (1 UMMZ). MARIPIPI: site M1 (3 UMMZ).

Haplonycteris fischeri Lawrence, 1939

Fischer's pygmy fruit bat is a Philippine endemic that occurs throughout the archipelago with the probable exception of the Palawan faunal region. It is found almost exclusively in primary forest and lightly disturbed forest and is typically most abundant at middle elevations (Heaney et al., 1989; Heideman & Heaney, 1989). On Leyte, we netted specimens between 300 m and 950 m on Mt. Pangasugan. It was uncommon in lowland forest at 300 and 500 m (sites L3 and L4) and common in lower montane forest and ridgetop mossy forest at 700 and 950 m elevation (sites L5 and L6; table 5). On Biliran, *Haplonycteris* was abundant in primary montane forest at 850 m (site B3), less com-

TABLE 6. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
9.1±0.70 (8.1–9.9)	7.8±0.29 (7.5–8.3)	19.7±0.57 (19.2–20.5)	–	–	–	–	–	–
8.6±0.30 (8.1–9.1)	7.4±0.20 (7.1–7.7)	18.3±0.58 (17.4–19.2)	–	–	–	–	–	–
9.3	7.9	19.5	143	18	23	24	74	73
9.0	7.6	19.0	151	27	21	22	82	68
8.6±0.38 (8.2–9.2)	7.5±0.23 (7.1–7.7)	18.7±0.44 (17.9–19.1)	135±8.4 (124–145)	14±2.1 (13–18)	20±1.2 (18–21)	21±1.7 (19–23)	74±2.8 (71–79)	69±12.8 (57–90)
8.5±0.46 (7.8–9.3)	7.6±0.30 (7.2–8.2)	18.3±0.71 (16.8–18.9)	128±5.0 (121–137)	15±2.1 (12–18)	20±0.9 (19–21)	21±1.1 (19–22)	74±2.6 (70–77)	58±8.9 (43–70)
8.8	7.7	18.1	137	16	19	21	73	72
8.6 (8.5–8.7)	7.4 (7.3–7.4)	18.3 (18.1–18.5)	125 (122–128)	14 (13–16)	18 (18–19)	22 (21–22)	73	51
6.0±0.18 (5.7–6.2)	5.1±0.22 (4.9–5.6)	11.6±0.51 (10.7–12.2)	73±3.9 (70–80)	0	12±1.0 (11–13)	14±0.6 (13–14)	48±0.8 (47–49)	18±1.0 (17–19)
5.9±0.18 (5.5–6.0)	5.1±0.18 (4.9–5.3)	11.5±0.33 (11.0–12.0)	70±1.5 (68–71)	0	11±0.5 (11–12)	14±0.5 (13–14)	49±0.8 (48–50)	18±1.3 (16–19)
5.9±0.24 (5.5–6.2)	5.2±0.34 (4.8–5.8)	11.8±0.44 (11.0–12.3)	73±3.3 (68–77)	0	13±1.0 (12–14)	14±1.0 (12–15)	49±1.6 (47–52)	18±1.4 (17–21)
5.8±0.22 (5.4–6.3)	5.4±0.33 (4.5–5.8)	12.0±0.49 (10.9–12.6)	74±2.9 (68–79)	0	13±1.2 (11–15)	14±0.7 (13–15)	50±2.0 (44–53)	19±1.6 (16–21)

mon in lightly disturbed lowland forest at 700 m (site B2), and rare in mixed forest plantation and agricultural land at 400 m (site B1; table 5). Despite considerable netting effort in forest habitat that was apparently excellent for them (65 net-nights; sites M1, M3, and M4), we took no *Haplonycteris* on Maripipi and doubt that they occur there. Females collected from mid-March to late April contained single embryos (crown–rump lengths = 3–4 mm) in arrested early development (Heideman, 1988, 1989). Large series of specimens from Leyte and Biliran show no indication of sexual size dimorphism (table 6). Leyte specimens are similar in body size to those from Dinagat, Catanduanes, and Luzon (Heaney & Rabor, 1982; Heaney et al., 1991), whereas those from Biliran are slightly larger. Specimens from Leyte and Biliran have karyotypes of 2n = 58, FN ≈ 66, possessing the highest known diploid number for the suborder Megachiroptera (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 94. LEYTE: Leyte Prov.: site L3 (2 USNM); site L4 (3 UMMZ, 1 USNM, 1 VISCA); site L5 (1 PNM, 2 UMMZ, 10 USNM); site L6 (3 USNM); site L12 (7 DMNH). BILIRAN: site B1 (2 USNM); site B2 (26 UMMZ); site B3 (2 PNM, 1 SU, 19 USNM, 1 VISCA, 4 WAM); site B4 (9 UMMZ).

Harpyionycteris whiteheadi whiteheadi Thomas, 1896

The harpy fruit bat is endemic to the Philippines, with prior records from Camiguin, Mindanao, Mindoro, and Negros islands (Peterson & Fenton, 1970; see also Koopman, 1989, who considered *H. celebensis* of Sulawesi to be conspecific). On Negros, it probably is restricted to primary forest and very lightly disturbed forest and is most common at middle elevations (Heaney et al., 1989; Heideman & Heaney, 1989). On Mt. Pangasugan,

TABLE 7. Means (± SD) and ranges of selected measurements of adult fruit bats (*Harpyionycteris* and *Macroglossus*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth	Rostral length	Orbital length	C to last M
Harpyionycteris whiteheadi										
Leyte	♂	7	41.0±0.56 (40.3–41.7)	23.3±0.46 (22.9–24.1)	6.4±0.45 (5.6–6.9)	5.7±0.56 (5.2–6.7)	15.4±0.41 (14.8–15.8)	11.4±0.23 (11.0–11.7)	17.4±0.29 (17.1–17.9)	15.9±0.28 (15.6–16.3)
	♀	3	40.6 (39.7–41.5)	23.3 (22.5–24.2)	6.5 (6.1–6.9)	5.6 (5.6–5.7)	15.3 (15.0–15.6)	11.1 (11.0–11.1)	17.3 (16.1–18.1)	15.6 (15.5–15.6)
Macroglossus minimus										
Leyte	♂	3	25.0 (24.5–25.8)	15.3 (14.5–16.2)	5.0 (4.8–5.3)	7.1 (6.8–7.4)	10.2 (9.9–10.8)	9.7 (9.3–10.4)	8.2 (7.9–8.4)	8.7 (8.2–9.4)
	♀	7	25.0±0.63 (23.8–25.7)	14.0±0.21 (13.8–14.4)	4.9±0.27 (4.4–5.2)	7.2±0.17 (7.0–7.4)	10.0±0.22 (9.6–10.2)	9.5±0.35 (9.1–10.0)	8.0±0.17 (7.8–8.3)	8.6±0.38 (8.1–9.0)
Biiran	♂	7	25.1±0.38 (24.6–25.7)	15.1±0.34 (14.7–15.6)	4.9±0.24 (4.4–5.1)	6.9±0.35 (6.4–7.3)	10.1±0.42 (9.5–10.7)	9.8±0.29 (9.5–10.2)	8.1±0.17 (7.9–8.4)	8.9±0.36 (8.5–9.6)
	♀	5	25.0±0.72 (23.9–25.7)	13.9±0.50 (13.4–14.6)	4.6±0.30 (4.3–4.9)	7.3±0.33 (7.0–7.8)	10.0±0.25 (9.7–10.4)	9.6±0.38 (9.0–10.0)	8.0±0.34 (7.7–8.6)	8.7±0.33 (8.3–9.4)
Maripipi	♂	4	24.9±0.78 (24.1–25.6)	15.2±0.68 (14.4–15.9)	4.8±0.25 (4.5–5.1)	7.0±0.25 (6.7–7.3)	10.5±0.25 (10.1–10.7)	9.5±0.34 (9.0–9.8)	8.1±0.22 (7.8–8.3)	8.6±0.33 (8.2–9.0)
	♀	3	25.1 (24.7–25.4)	14.4	4.7 (4.6–4.8)	7.0 (6.5–7.5)	10.1 (9.6–10.4)	9.4 (9.4–9.5)	8.1 (7.8–8.3)	8.3 (7.5–8.7)

Note: Measurements other than weight are in millimeters.

Leyte, it was confined to undisturbed primary forest, where it was rare at 300 m (site L3) and moderately common at 500 m and 700 m elevation (sites L4 and L5; table 5). On Biliran, we netted one specimen in partially logged primary montane forest at 920 m elevation (site B4). We also heard the distinctive whistling flight calls of this species in primary forest at elevations from 600 to 950 m elevation (site B3). On Maripipi, we captured two specimens in primary mossy forest at 800 m elevation (site M3). Pregnant females captured between 20 March and 8 May contained single embryos (crown–rump lengths = 8–50 mm). Four lactating females taken between 18 and 30 March had recently given birth to single offspring. Three of these, weighing 110, 110, and 125 g, were carrying nursing young weighing 26, 21, and 21 g, respectively. Cranial and external measurements of males average slightly larger than those of females (table 7). This species has a distinctive karyotype of 2n = 36, FN = 58 (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 29. LEYTE: Leyte Prov.: site L3 (1 USNM); site L4 (4 UMMZ, 6 USNM, 1 VISCA); site L5 (1 PNM, 11 USNM); site L11 (1 UPLB); site L12 (1 UPLB). BILIRAN: site B4 (1 UMMZ). MARIPIPI: site M3 (2 UMMZ).

Macroglossus minimus lagochilus (Matschie, 1899)

The dagger-toothed flower bat occurs from Thailand to Australia and is found throughout the Philippines. On Leyte, we netted this species in primary lowland, montane, and mossy forest at elevations ranging from 300 to 950 m and in disturbed lowland forest between 50 and 100 m elevation (table 5). It was found at all forest and second growth sites on Biliran and Maripipi (table 5). Although we encountered it at virtually all of our netting sites, *M. minimus* is most common in disturbed habitats (Heaney et al., 1989; Heideman & Heaney, 1989). Most specimens were netted within 25 m of wild or domestic bananas and abaca (*Musa* spp.), whose flowers represent an important food source for this nectarivorous species. We collected females pregnant with single embryos from late March to early July. On average, males in our series are slightly larger than females in most cranial and external dimensions (table 7). Size ranges are comparable to those seen for series from several other Philippine islands (Heaney & Rabor, 1982; Heaney, 1984; Heaney et al., 1991). The species has a standard karyotype of 2n = 34, FN = 62, that is identical to those from elsewhere in

TABLE 7. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
12.0±0.29 (11.6–12.3)	8.0±0.11 (7.4–8.2)	20.9±0.29 (20.6–21.3)	139±5.3 (130–145)	0	23±1.5 (21–25)	22±1.2 (20–24)	84±2.7 (80–87)	100±5.6 (88–104)
11.8 (11.8–11.9)	7.6 (7.4–7.8)	20.6 (20.4–20.8)	139 (133–143)	0	23 (22–23)	21 (20–22)	82 (81–83)	110
5.3 (5.1–5.7)	5.2 (5.2–5.3)	13.4 (13.2–13.7)	74 (70–78)	0	12 (11–13)	16 (16–17)	44 (42–45)	18 (16–20)
5.3±0.22 (5.0–5.6)	5.1±0.14 (5.0–5.4)	13.7±0.35 (13.1–14.1)	73±1.8 (70–76)	0	12±0.8 (11–13)	16±1.2 (14–17)	42±1.4 (40–44)	17±1.7 (16–20)
5.4±0.29 (5.0–5.7)	5.0±0.22 (4.8–5.4)	13.8±0.28 (13.4–14.1)	71±2.6 (67–73)	0	13±1.0 (12–14)	16±0.6 (15–16)	42±0.5 (42–43)	17±1.0 (16–18)
5.3±0.23 (5.1–5.6)	5.1±0.24 (4.8–5.4)	13.5±0.48 (13.0–14.1)	68±2.1 (66–70)	0	12	16±1.2 (15–17)	41±1.2 (40–42)	16±0.6 (15–16)
5.1±0.19 (5.0–5.4)	4.9±0.13 (4.8–5.1)	13.0±0.43 (12.5–13.5)	68±1.9 (67–71)	0	12±0.8 (11–13)	16±1.0 (15–17)	42±0.6 (41–42)	18±2.0 (16–20)
5.1 (5.0–5.1)	5.1 (5.0–5.3)	13.4 (13.4–13.5)	70 (66–74)	0	13 (12–14)	17 (15–18)	42 (41–44)	18 (17–19)

the species' distributional range (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 87. LEYTE: Leyte Prov.: site L2 (3 PNM, 17 USNM); site L3 (4 USNM); site L4 (1 UMMZ, 3 USNM, 1 VISCA); site L5 (4 UMMZ, 4 USNM); site L6 (1 USNM). BILIRAN: site B1 (2 PNM, 3 USNM); site B2 (10 UMMZ); site B3 (1 SU, 7 USNM, 1 VISCA); site B4 (4 UMMZ). MARIPIPI: site M1 (4 UMMZ); site M2 (1 UMMZ); site M3 (1 UMMZ); site M4 (15 USNM).

OTHER RECORDS—LEYTE: site L11 (ROM); site L15 (AMNH).

Ptenochirus jagori (Peters, 1861)

This species is a Philippine endemic, occurring throughout the archipelago with the exception of the Palawan region. It was abundant on Mt. Pangasugan in disturbed secondary forest at 50 m elevation (site L2) and in primary lowland forest at 300 m and 500 m (sites L3 and L4). It was rare in montane forest at 700 m (site L5) and absent in mossy forest at 950 m (site L6; table 5; Heaney et al., 1989). It was also present on the campus of the Visayas State College of Agriculture near areas of secondary forest (site L1). We observed this species roosting in small solution pits (ca. 20–30 cm across and 30–70 cm deep) along the cliff face at the entrance to Cathedral Cave (site L7). Bats were well shaded within these cavities but were clearly visible from below. We found eight groups in such pits, each containing from 1 to 10 individuals. Below each roost was a pile of chewed and spat-out remains of fruit, primarily figs (*Ficus*). These piles of ejecta were large (1.2–1.6 m in diameter and up to 25 cm thick), indicating long-term use of the roost sites. We also found two small groups of *P. jagori* inside two of the caves, both in solution pits in well-lit places near the entrances. On Biliran, this species was abundant in partially logged lowland primary forest at 700 m (site B2) and in the mixed agricultural/replanted forest area at 450 m elevation (site B1) but uncommon in primary montane and mossy forest at 850 m and 920 m (sites B3 and B4; table 5). *Ptenochirus jagori* was found in all habitats sampled on Maripipi (table 5). We collected females pregnant with single embryos from early March to early July. In our series, males are consistently larger than females in most cranial dimensions (table 8). There is also substantial geographic variation in body size: specimens from Leyte and Biliran are

TABLE 8. Means (± SD) and ranges of selected measurements of adult fruit bats (*Ptenochirus*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth	Rostral length	Orbital length	C to last M
Ptenochirus jagori										
Leyte	♂	11	35.5±0.85 (34.2–36.6)	24.9±0.75 (23.5–25.8)	7.2±0.46 (6.5–8.0)	6.3±0.16 (6.1–6.5)	14.5±0.35 (14.0–15.1)	10.8±0.46 (10.2–11.8)	15.9±0.62 (14.6–16.7)	12.5±0.46 (12.0–13.2)
	♀	13	34.7±0.80 (33.3–36.1)	24.1±0.74 (23.2–25.8)	7.0±0.36 (6.5–7.8)	6.3±0.36 (5.8–7.0)	14.3±0.40 (13.7–15.1)	10.3±0.39 (9.6–11.0)	15.8±0.56 (14.9–16.7)	12.1±0.31 (11.3–12.4)
Biliran	♂	10	35.0±0.64 (34.1–35.7)	24.3±0.76 (23.0–25.7)	7.1±0.42 (6.4–7.8)	6.4±0.41 (5.8–7.0)	14.5±0.38 (13.9–15.2)	10.6±0.35 (10.2–11.2)	15.7±0.43 (14.9–16.3)	12.3±0.32 (11.8–12.8)
	♀	9	34.1±0.52 (33.2–34.6)	24.0±0.58 (23.0–24.8)	7.0±0.28 (6.6–7.5)	6.5±0.29 (6.0–6.9)	14.4±0.37 (13.8–14.8)	10.4±0.44 (9.5–11.0)	15.4±0.30 (15.0–15.7)	11.8±0.24 (11.4–12.1)
Maripipi	♂	4	36.4±0.88 (35.4–37.1)	25.3±0.83 (24.7–26.5)	7.9±0.51 (7.1–8.2)	6.0±0.49 (5.5–6.6)	14.9±0.39 (14.6–15.4)	11.7±0.41 (11.3–12.1)	16.0±0.38 (15.5–16.4)	12.4±0.60 (12.0–13.3)
	♀	6	35.2±1.06 (33.9–36.7)	24.2±0.65 (23.8–25.4)	7.2±0.32 (6.9–7.6)	6.1±0.20 (5.8–6.4)	14.5±0.18 (14.2–14.7)	10.7±0.50 (9.9–11.3)	15.9±0.40 (15.3–16.5)	12.2±0.21 (12.0–12.5)
Ptenochirus minor										
Leyte	♂	15	29.0±0.82 (28.1–30.6)	19.6±0.84 (18.2–20.3)	6.1±0.30 (5.6–6.7)	6.3±0.38 (5.8–7.2)	12.5±0.31 (12.0–12.8)	9.0±0.39 (8.5–9.8)	12.5±0.31 (11.8–13.3)	10.1±0.25 (9.5–10.5)
	♀	17	28.7±0.83 (27.2–30.4)	19.4±0.55 (18.3–20.4)	6.1±0.32 (5.3–6.6)	6.1±0.33 (5.5–6.6)	12.5±0.29 (11.9–12.9)	8.9±0.41 (8.1–9.6)	12.5±0.45 (11.5–13.2)	9.9±0.22 (9.5–10.4)
Biliran	♂	12	29.2±0.58 (28.4–30.1)	19.6±0.81 (18.2–21.0)	6.2±0.34 (5.8–7.0)	6.2±0.28 (5.8–6.7)	12.3±0.23 (11.8–12.6)	9.1±0.32 (8.5–9.7)	12.6±0.34 (12.1–13.4)	10.3±0.34 (9.8–10.8)
	♀	12	28.5±0.63 (27.8–30.2)	19.1±0.41 (18.7–20.1)	6.0±0.26 (5.7–6.6)	6.2±0.34 (5.6–6.8)	12.2±0.38 (11.5–12.6)	8.7±0.38 (8.2–9.5)	12.4±0.30 (12.0–13.1)	9.9±0.28 (9.5–10.3)

Note: Measurements other than weight are in millimeters.

larger than those from Camiguin, Catanduanes, and Luzon in most cranial and external dimensions but substantially smaller than those from Maripipi and Dinagat (Heaney & Rabor, 1982; Heaney, 1984; Heaney et al., 1991). Leyte specimens have a karyotype of 2n = 44, FN ≈ 56 (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 186. LEYTE: Leyte Prov.: site L1 (9 USNM); site L2 (6 PNM, 21 USNM); site L3 (14 USNM); site L4 (2 SU, 12 UMMZ, 14 USNM, 2 VISCA, 2 WAM); site L5 (2 USNM); site L7 (1 UMMZ, 4 USNM); site L9 (21 DMNH). BILIRAN: site B1 (2 PNM, 15 USNM, 1 WAM); site B2 (27 UMMZ); site B3 (2 USNM); site B4 (3 UMMZ). MARIPIPI: site M1 (10 UMMZ); site M2 (6 UMMZ); site M4 (10 USNM).

OTHER RECORDS—LEYTE: site L11 (ROM).

Ptenochirus minor Yoshiyuki, 1979

This poorly known endemic is one of the most recently described species of Philippine mammals (Yoshiyuki, 1979). It is clearly distinguishable from *P. jagori* by its smaller body size (table 8), distinct karyotype of 2n = 46, FN ≈ 56 (Rickart et al., 1989a), and habitat preference (table 5). The species was known previously only from Dinagat and Mindanao, with a probably erroneous record from Palawan (Heaney et al., 1987). On the Mt. Pangasugan transect, this species was abundant in lowland, montane, and mossy primary forest between 300 and 950 m elevation (sites L3–L6) and was common in secondary forest at 50 m elevation (site L2; table 5; Heaney et al., 1989). It was not encountered on the campus of the Visayas State College of Agriculture and was rare in nearby agricultural areas (site L1). On Biliran, this was the most abundant pteropodid bat in undisturbed and in partially disturbed lowland and montane forest between 700 and 850 m elevation (sites B2–B4) but was not found in forest plantation or in a small patch of remnant forest at 400 m elevation (site B1; table 5). *Ptenochirus minor* was not taken on Maripipi, despite considerable netting effort in apparently suitable forest habitat (80 net-nights; sites M1–M4). We believe that it does not occur on that island. On Leyte, one specimen was collected from a daytime roost in the foliage of a tree ca. 10 m

TABLE 8. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
8.9±0.33	8.0±0.23	17.7±0.62	135±5.2	12±2.6	22±1.0	20±1.2	80±5.3	75±2.9
(8.3–9.5)	(7.7–8.4)	(16.9–18.8)	(130–140)	(9–14)	(21–23)	(19–21)	(72–83)	(72–78)
8.6±0.19	7.7±0.25	17.3±0.59	130±3.5	12±1.9	20±0.9	21±1.0	85±2.0	71±5.0
(8.3–8.9)	(7.2–8.1)	(16.6–18.3)	(125–134)	(10–14)	(19–22)	(20–22)	(82–88)	(62–78)
8.7±0.28	7.8±0.21	17.8±0.34	129±4.0	12±1.4	22±0.7	21±1.0	82±1.5	72±2.3
(8.2–9.0)	(7.5–8.1)	(17.3–18.3)	(122–135)	(10–14)	(21–23)	(20–23)	(80–85)	(69–77)
8.4±0.16	7.8±0.29	17.2±0.62	127±3.6	11±1.9	22±0.7	21±1.0	81±2.2	71±5.7
(8.1–8.6)	(7.3–8.1)	(16.1–18.1)	(120–131)	(6–12)	(21–22)	(19–22)	(78–84)	(61–79)
8.7±0.45	8.2±0.30	18.3±0.66	138±2.8	12±1.7	21±1.3	21±1.4	86±2.7	86±10.4
(8.3–9.3)	(7.7–8.3)	(17.5–19.1)	(135–140)	(10–14)	(20–23)	(19–22)	(84–90)	(72–94)
8.6±0.19	7.9±0.20	17.8±0.45	134±4.6	13±0.4	22±1.7	22±1.5	85±2.0	93±7.6
(8.3–8.8)	(7.7–8.2)	(17.1–18.4)	(128–141)	(12–13)	(20–24)	(20–24)	(83–87)	(81–102)
7.1±0.18	6.5±0.27	14.5±0.52	104±4.9	9±2.1	16±0.6	18±1.2	65±3.0	36±5.0
(6.7–7.5)	(6.1–7.0)	(13.8–15.5)	(98–113)	(5–11)	(15–16)	(15–19)	(64–70)	(29–47)
7.0±0.15	6.5±0.24	14.3±0.42	106±3.8	9±1.8	16±1.0	18±1.4	66±2.0	36±3.9
(6.8–7.3)	(6.1–7.0)	(13.6–15.0)	(102–114)	(4–10)	(14–17)	(16–18)	(62–69)	(28–42)
7.2±0.32	6.6±0.27	14.9±0.45	104±2.8	9±1.5	17±0.7	18±1.1	66±2.2	37±3.9
(6.7–7.7)	(6.1–7.0)	(14.0–15.7)	(100–110)	(8–12)	(16–18)	(17–20)	(63–71)	(32–44)
7.0±0.23	6.5±0.20	14.3±0.41	104±2.8	9±1.5	17±1.2	18±1.0	66±2.6	36±2.6
(6.7–7.4)	(6.2–6.8)	(13.7–15.3)	(100–109)	(6–12)	(15–19)	(17–20)	(61–71)	(33–42)

above the ground in secondary forest (near site L2). Females pregnant with single embryos were taken from early March to late May. Males in our series are slightly larger than females in most cranial measurements (table 8). Cranial and external measurements for specimens from Leyte and Biliran are comparable but are substantially smaller than those for a series from Dinagat (Heaney & Rabor, 1982).

SPECIMENS EXAMINED—Total 177. LEYTE: Leyte Prov.: site L1 (4 USNM); site L2 (1 PNM, 7 USNM); site L3 (22 USNM, 1 WAM); site L4 (23 UMMZ, 21 USNM, 2 VISCA); site L5 (4 PNM, 2 SU, 5 UMMZ, 23 USNM); site L6 (1 USNM). BILIRAN: site B2 (24 UMMZ); site B3 (2 PNM, 1 SU, 23 USNM, 1 VISCA); site B4 (10 UMMZ).

Pteropus hypomelanus cagayanus Mearns, 1905

This common flying fox occurs from the Maldive Islands to the Solomon Islands (Koopman, 1989). It is widespread in the Philippines, where it is most commonly encountered in lowland agricultural areas. It was first reported from Leyte by Steere (1890). We collected none during our field work on Leyte or Biliran. However, we observed this species feeding at fruiting mabolo trees (*Diospyros* sp.) on the campus of the Visayas State College of Agriculture (site L1). On Maripipi, we netted two specimens near a fruiting fig (*Ficus*) in a partial clearing on a ridge in primary forest at 600 m elevation (site M4). In April 1987 we observed and collected specimens at two roost trees in a coconut grove at 50 m elevation on Maripipi (site M8). The two roosts each held 50–75 individuals, which appeared to be evenly dispersed throughout the crowns. We observed paired agonistic encounters involving threats and boxing with closed wings. In such cases, one individual usually retreated within a short time; we never saw encounters escalate to biting or clawing. When disturbed by us, all individuals quickly left the roost and dispersed in small groups to new roosts in nearby trees and coconut palms. Many individuals at both roosts were carrying dependent young. On 23 April we collected three adult males and two immature yearling females at this site. On the same

TABLE 9. Means (± SD) and ranges of selected measurements of adult fruit bats (*Pteropus* and *Rousettus*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Post-orbital width	Mastoid breadth	Rostral length	Orbital length	C to last M
Pteropus hypomelanus										
Leyte	♂	1	61.7	33.6	9.6	8.1	20.1	20.1	24.1	22.8
Maripipi	♂	3	61.8 (60.8–62.4)	34.7 (33.8–35.6)	8.8 (8.4–9.1)	7.2 (7.1–7.3)	20.6 (19.8–21.3)	21.9 (21.5–22.1)	24.5 (24.0–24.9)	23.3 (22.5–24.3)
Pteropus pumilus										
Maripipi	♂	5	49.0±1.20 (47.5–50.8)	28.0±0.54 (27.2–28.7)	7.4±0.27 (7.1–7.8)	7.9±0.70 (7.3–9.0)	17.6±0.30 (17.2–18.0)	17.0±0.87 (16.1–18.4)	19.5±0.25 (19.2–19.7)	18.3±0.68 (17.6–19.3)
	♀	4	47.4±0.59 (46.9–48.1)	27.6±0.71 (26.8–28.5)	7.1±0.17 (6.9–7.3)	7.5±0.42 (6.9–7.8)	17.3±0.25 (17.0–17.6)	16.3±0.23 (16.1–16.5)	18.9±0.46 (18.3–19.4)	17.9±0.45 (17.5–18.1)
Pteropus vampyrus										
Leyte	♂	7	76.5±1.78 (73.9–78.9)	43.7±1.29 (41.5–45.0)	10.8±0.54 (9.9–11.3)	9.5±0.36 (9.1–9.9)	24.5±0.69 (23.6–25.2)	27.6±0.98 (26.1–29.1)	31.1±0.82 (29.3–31.6)	28.9±2.05 (28.3–31.5)
	♀	4	75.4±2.12 (72.3–76.8)	41.9±2.40 (39.6–44.4)	10.2±0.69 (9.2–10.8)	9.0±0.85 (8.4–10.2)	23.7±0.92 (23.2–24.8)	26.5±0.98 (25.5–27.8)	30.5±1.02 (29.3–31.6)	29.2±1.09 (28.5–30.8)
Rousettus amplexicaudatus										
Leyte	♂	4	37.6±0.83 (37.0–38.8)	23.5±0.42 (22.9–23.9)	8.4±0.28 (8.1–8.7)	7.6±0.21 (7.4–7.8)	14.3±0.21 (14.0–14.5)	14.4±0.73 (13.8–15.3)	14.7±0.25 (14.4–15.0)	13.5±0.47 (13.2–14.2)
	♀	9	35.7±0.72 (34.5–36.5)	21.9±0.63 (20.9–22.9)	7.9±0.53 (7.3–8.7)	7.3±0.45 (6.9–8.1)	13.8±0.48 (12.8–14.6)	13.2±0.39 (12.8–13.9)	14.1±0.56 (13.1–15.0)	12.8±0.36 (12.1–13.2)
Biliran	♂	5	37.2±0.57 (36.4–37.7)	23.5±0.88 (22.3–24.7)	8.2±0.23 (8.0–8.5)	7.6±0.42 (7.2–8.1)	14.4±0.44 (13.9–14.9)	14.1±0.57 (13.4–14.9)	14.5±0.19 (14.2–14.7)	13.2±0.26 (12.9–13.6)
	♀	8	35.6±0.66 (34.5–36.5)	21.8±0.43 (21.2–22.4)	8.0±0.30 (7.6–8.5)	7.7±0.66 (6.8–8.9)	13.8±0.44 (13.2–14.7)	13.4±0.74 (12.0–14.2)	13.9±0.43 (13.2–14.3)	13.0±0.47 (12.5–13.9)
Maripipi	♂	2	37.6 (35.5–38.3)	22.2 (21.6–22.7)	7.7 (7.1–8.3)	7.2 (7.0–7.4)	13.7 (13.4–13.9)	13.8 (13.0–14.6)	14.2 (13.6–14.7)	13.6 (13.1–14.0)
	♀	6	35.8±0.26 (35.4–36.1)	21.9±1.01 (20.1–23.0)	8.3±0.41 (7.8–9.0)	7.6±0.45 (7.2–8.3)	13.9±0.42 (13.3–14.6)	13.4±0.42 (12.8–14.0)	14.3±0.33 (13.7–14.7)	12.9±0.23 (12.6–13.2)

Note: Measurements other than weight are in millimeters.
* Measured from dry skins.

date we obtained a lactating adult female with its dependent juvenile and a second juvenile from local hunters. These specimens were shot at a similar roost site several kilometers from the first roost (site M7). Cranial measurements (table 9) are similar to those for specimens from Camiguin, Dinagat, and Panay (Heaney & Rabor, 1982; Heaney, 1984). This species has a karyotype of 2n = 38, FN = 72 (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 11. LEYTE: unknown locality (1 UMMZ). MARIPIPI: site M4 (2 USNM); site M7 (3 USNM); site M8 (5 USNM).

Pteropus pumilus Miller, 1910

The little golden-mantled flying fox is a Philippine endemic. It occurs throughout the archipelago with the exception of the Palawan region. The species was revised by Klingener and Creighton (1984), who included *P. tablasi* and *P. balutus* as synonyms. *Pteropus pumilus* apparently is restricted to areas in or near primary forest, where it may be locally common (Heideman & Heaney, 1989). We did not encounter it on Leyte, but D. Empesso collected specimens in Hindang Municipality in 1963 (near site L7). It was not recorded on Biliran, but few of our nets were set in areas that are generally suitable for capturing it (Heideman & Heaney, 1989). The species was moderately abundant on Maripipi, where we netted specimens at all of our collecting sites in disturbed and primary lowland, montane, and mossy forest between 350 and 800 m elevation (sites M1–M4). In 1984 we saw a single individual roosting in disturbed forest at 650 m elevation (site M2). It was hanging from a frond in a 5 m tree fern in an open area lacking concealing vegetation. The bat remained at this roost from at least mid-afternoon to evening, including a 2 hr period of light

TABLE 9. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
17.0	12.0	34.0	–	0	–	–	137	–
16.0 (15.7–16.5)	12.8 (12.4–13.2)	34.6 (34.3–34.7)	224 (212–236)	0	44 (41–49)	32 (31–32)	141 (138–144)	438 (425–450)
13.0±0.48 (12.2–13.4)	9.7±0.23 (9.4–9.9)	26.3±0.91 (25.3–27.6)	168±2.9 (166–173)	0	36±3.4 (31–40)	24±1.1 (23–26)	108±3.8 (103–113)	189±7.6 (180–197)
12.9±0.45 (12.2–13.2)	9.8±0.50 (9.5–10.5)	25.7±0.31 (25.4–26.1)	160±2.4 (158–163)	0	36±4.4 (29–38)	26±2.2 (23–28)	104±3.0 (103–109)	166±4.9 (160–172)
20.0±0.75 (19.2–21.4)	15.0±0.83 (14.0–16.4)	42.2±0.75 (41.5–43.5)	314±6.6 (307–315)	0	54±3.5 (52–58)	38±7.1 (30–44)	190±8.5 (179–202)	–
20.2±1.01 (19.4–21.7)	15.3±0.62 (14.5–15.9)	41.3±0.87 (40.1–42.1)	–	0	–	–	190±9.2* (183–204)	–
10.5±0.43 (10.1–11.1)	7.9±0.08 (7.8–8.0)	19.9±0.76 (19.2–20.9)	146±4.7 (142–151)	18±2.4 (15–20)	22±1.5 (21–24)	22±1.7 (20–24)	90±1.5 (88–91)	97±5.4 (91–104)
9.9±0.35 (9.3–10.3)	7.9±0.29 (7.6–8.5)	18.5±0.48 (17.5–19.0)	143±5.2 (136–152)	18±2.6 (15–22)	22±1.3 (20–24)	21±0.7 (20–22)	88±3.4 (81–92)	86±8.8 (68–100)
9.7±0.28 (9.3–10.0)	8.4±0.18 (8.2–8.6)	19.3±0.24 (18.9–19.5)	149±2.4 (147–153)	19±3.1 (16–23)	24±0.4 (24–25)	22	88±0.9 (86–88)	100±4.2 (95–106)
9.7±0.40 (9.1–10.3)	8.2±0.12 (8.1–8.4)	18.5±0.61 (17.6–19.4)	141±3.2 (137–146)	17±2.1 (13–20)	23±1.2 (22–25)	21±0.9 (20–22)	85±1.6 (83–87)	77±2.9 (72–81)
10.0 (9.6–10.4)	8.4 (7.8–8.9)	19.1 (18.3–19.8)	144 (143–146)	18 (17–18)	24	22 (21–23)	86 (84–87)	82 (77–87)
9.7±0.15 (9.5–9.9)	8.5±0.35 (8.0–9.0)	18.3±0.54 (17.7–19.1)	142±3.4 (137–146)	17±2.1 (13–19)	24±1.4 (22–26)	22±0.8 (21–23)	86±2.4 (83–88)	74±3.8 (68–80)

rain, during which time it groomed and licked off water droplets. The roost was not used on subsequent days. We collected lactating females in late April and early May. Males in our series are consistently larger than females in most cranial and external measurements (table 9).

SPECIMENS EXAMINED—Total 20. MARIPIPI: site M1 (6 UMMZ); site M2 (6 UMMZ); site M3 (2 UMMZ); site M4 (5 USNM); site M10 (1 UMMZ).

OTHER RECORDS—LEYTE: site L7 (ROM).

Pteropus vampyrus lanensis Mearns, 1905

The giant flying fox is widespread in Southeast Asia and is locally common in primary forest throughout the Philippines. The species was first reported from Leyte by Steere (1890), and specimens have been recorded from Tambis and Patok (sites L9 and L10). Although we did not collect any specimens, some of the bats we observed feeding in mabolo trees (*Diospyros*) on the campus of the Visayas State College of Agriculture (site L1) probably were this species. Local residents reported that large flying foxes were commonly seen at this site. There are no specimens from either Biliran or Maripipi. In the Leyte series, males are consistently larger than females in most cranial measurements (table 9).

SPECIMENS EXAMINED—Total 14. LEYTE: Leyte Prov.: site L9 (10 DMNH); site L10 (2 AMNH); specific locality unknown (2 FMNH).

Rousettus amplexicaudatus amplexicaudatus (E. Geoffroy, 1810)

The rousette fruit bat occurs from Thailand to the Solomon Islands and is found throughout the

TABLE 10. The number of microchiropterans netted at principal sites on Leyte, Biliran, and Maripipi islands.

Species	Leyte					Biliran				Maripipi		
	L2 (50 m)	L3 (300 m)	L4 (500 m)	L5 (700 m)	L6 (950 m)	B1 (450 m)	B2 (700 m)	B3 (850 m)	B4 (920 m)	M1 (400 m)	M2 (700 m)	M4 (740 m)
Emballonura alecto	0	1	0	0	0	0	0	0	0	0	0	0
Megaderma spasma	0	0	3	3	0	0	0	2	0	0	0	0
Hipposideros diadema	6	0	2	0	0	0	0	0	0	0	0	0
Hipposideros obscurus	0	0	0	0	0	0	0	0	0	0	1	4
Rhinolophus arcuatus	0	0	2	0	0	1	0	5	0	0	0	2
Rhinolophus inops	1	0	27	6	6	9	0	62	0	0	0	0
Rhinolophus virgo	0	0	4	0	0	0	0	0	0	0	0	1
Harpiocephalus harpia	0	0	1	0	0	0	0	0	0	0	0	0
Kerivoula hardwickii	0	0	1	0	1	0	0	1	0	0	0	0
Miniopterus schreibersii	0	0	4	1	0	0	0	0	0	0	0	0
Miniopterus tristis	1	0	0	0	0	0	0	0	0	0	0	0
Murina cyclotis	0	0	0	0	0	0	1	0	0	0	0	0
Myotis muricola	1	0	1	0	0	1	3	1	0	0	0	0
Philetor brachypterus	0	0	2	0	0	0	0	0	0	0	0	0
Scotophilus kuhlii	5	0	0	0	0	0	0	0	0	0	0	0
Total captures	14	1	47	10	7	11	4	71	0	0	1	7
Total net-nights	25	77	79	123	33	8	25	74	4–8	10	15	49
Number of species	5	1	10	3	3	3	2	5	0	0	1	3

Philippines. Although it may be found in forest habitats, it is most common in forest clearings and in agricultural lands (Heaney et al., 1989; Heideman & Heaney, 1989). On Mt. Pangasugan, Leyte, this species was uncommon in primary lowland and montane forest at 500 and 700 m elevation (sites L4 and L5). It was common in mixed secondary forest and agricultural land at 50 m (site L2) and was also present in residential areas on the campus of the Visayas State College of Agriculture (site L1). It was not taken in either mossy forest at 950 m or lowland forest at 300 m (table 5). On Biliran, the species was extremely abundant in disturbed forest and agricultural land at 450 m (site B1) but was not recorded at any primary forest sites (table 5). We also netted one specimen near some fruit trees in Naval town (site B5). A sea cave on Tincansan Island (site B7), immediately offshore from Biliran, supported a colony of more than 5,000 individuals. On Maripipi, we captured them in a wide range of habitats between 200 and 650 m elevation, but they were common only in second growth at 700 m (site M3; table 5). Our records indicate a very long breeding season. Females pregnant with single embryos were taken from early March to early July. Lactating females carrying dependent young were taken from late April to July. In late April we netted females with weights between 74 and 85 g that were carrying juveniles weighing from 15 to 24 g (between 19% and 28% of the maternal weight). Males of this species are consistently larger than females in most cranial and external measurements (table 9). Size ranges are similar to those reported for series from other Philippine islands (Heaney & Rabor, 1982; Heaney et al., 1991). The species has a karyotype of 2n = 36, FN = 68 (Rickart et al., 1989a).

SPECIMENS EXAMINED—Total 104. LEYTE: Leyte Prov.: site L1 (2 PNM, 1 SU, 5 USNM, 2 WAM); site L2 (1 PNM, 9 USNM); site L4 (1 SU, 1 UMMZ, 9 USNM); site L5 (2 USNM, 1 WAM); site L15 (1 AMNH); site L14 (1 AMNH). BILIRAN: site B1 (1 PNM, 37 USNM, 1 VISCA, 2 WAM); site B7 (13 UMMZ). MARIPIPI: site M1 (1 UMMZ); site M2 (11 UMMZ); site M4 (2 USNM).

Family **Emballonuridae**—Sheath-Tailed Bats

Emballonura alecto alecto (Eydoux & Gervais, 1836)

The sheath-tailed bat is a common cave-dwelling species that occurs throughout the Philippines and is also known from Borneo, the Moluccas, and Sulawesi (Koopman, 1989). We netted a single specimen on Mt. Pangasugan in primary lowland forest at 300 m (site L3; table 10). The species was very common in all of the small Cathedral caves (site L7), usually in cavities near the mouths of

the caves where there was dim light. Group size varied from singletons to about 100 individuals. On Biliran, we collected a group of four males in a rockfall cave at 500 m (site B6). We found groups of both sexes in five of the nine rockfall caves we visited on Maripipi (sites M11–M15); most colonies were small, but the largest (site M14) included ca. 60 individuals. Pregnant females containing single embryos were collected in early March on Leyte (crown–rump lengths = 4–9 mm) and during early April on Maripipi (crown–rump lengths = 11–14 mm). Lactating females and unweaned juveniles were collected in July 1981. There is no apparent sexual size dimorphism in this species. Specimens from Leyte appear to be slightly larger than those from Biliran and Maripipi in some cranial and external measurements (table 11).

SPECIMENS EXAMINED—Total 99. LEYTE: Leyte Prov.: site L3 (1 USNM); site L7 (1 PNM, 1 SU, 7 UMMZ, 41 USNM, 3 VISCA). BILIRAN: site B6 (4 USNM). MARIPIPI: site M11 (3 USNM); site M12 (1 USNM); site M13 (2 PNM, 11 USNM); site M14 (19 UMMZ); site M15 (5 UMMZ).

Taphozous melanopogon philippinensis Waterhouse, 1845

Tomb bats are widespread in southern Asia and are found throughout the Philippines. Described as a separate species by Waterhouse (1845), the Philippine form was arranged by Dobson (1878), without comment, as a subspecies of the widespread *T. melanopogon*. It was retained as a separate species by Hollister (1913), without comment, and by Lawrence (1939), who described differences in pelage color between *philippinensis* and *melanopogon*. Our comparison of large series of specimens from the Philippines and elsewhere in Asia does not confirm Lawrence's (1939) characters; therefore, we accept Dobson's (1878) arrangement. On Leyte, we found a colony of a few dozen *Taphozous* in one of the smaller Cathedral caves (site L7). The smaller cave on Tincanson Island immediately off the coast of Biliran (site B7) contained a colony of 200–400 individuals. Small groups were found in three rockfall caves on Maripipi (site M12). Although tomb bats are often abundant in urban and agricultural areas or in caves, our data indicate that they are rare in forested habitats. Females pregnant with single embryos in late term (crown–rump lengths = 20–27 mm) were collected on 19 April 1987. Lactating females were taken in early July 1981. No sexual or geographic variation in body size is apparent in this species within the Philippines (table 11).

SPECIMENS EXAMINED—Total 34. LEYTE: Leyte Prov.: site L7 (2 UMMZ, 1 VISCA, 2 WAM). BILIRAN: site B7 (18 UMMZ). MARIPIPI: site M12 (11 USNM).

Family **Megadermatidae**—False Vampire Bats

Megaderma spasma spasma (Linnaeus, 1758)

The false vampire bat occurs from India to the Moluccas and is found throughout the Philippines. On Leyte, we collected this species from one of the smaller caves of the Cathedral Cave complex (site L7). We captured one specimen from a small group roosting in a large hollow tree (*Ficus*) in primary lowland forest at 300 m elevation on Mt. Pangasugan (site L3). Others were netted in primary lowland and montane forest at 500 and 700 m elevation (sites L4 and L5; table 10). On Biliran, two specimens were netted in montane forest at 850 m elevation (site B3; table 10). None were taken on Maripipi. A female pregnant with a single embryo of 15 mm crown–rump length was taken on 21 March 1987. Sexual size dimorphism is not apparent in this species. Specimens from Leyte are slightly larger than two individuals from Mindanao but comparable in size to specimens from Dinagat and Catanduanes (table 11; Heaney & Rabor, 1982; Heaney, 1984).

SPECIMENS EXAMINED—Total 18. LEYTE: Leyte Prov.: site L3 (1 USNM); site L4 (2 USNM, 1 WAM); site L5 (3 USNM); site L7 (4 UMMZ, 1 VISCA); site L10 (4 AMNH). BILIRAN: site B3 (1 PNM, 1 USNM).

Family **Rhinolophidae**—Horseshoe Bats

Hipposideros ater Templeton, 1848

The dark leaf-nosed bat is found from India to northern Australia and is widespread in the Philippines (Hill et al., 1986; Koopman, 1989). On Maripipi, we collected 17 from a group of 30–40 individuals in a 2 m chamber in the deepest portion of a 10 m rockfall cave (site M12). The approaching passage had several sharp turns, so that the bats were roosting in almost complete darkness. The species was not encountered on either

TABLE 11. Means (± SD) and ranges of selected measurements of adult bats (Emballonuridae and Megadermatidae) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-incisive length	Zygomatic breadth	Inter-orbital width	Condylo-canine length	Mastoid breadth	Rostral length	Orbital length	C to last M
Emballonura alecto										
Leyte	♂	8	13.8±0.26 (13.4–14.2)	8.8±0.22 (8.4–9.0)	2.9±0.14 (2.6–3.0)	13.0±0.29 (12.6–13.3)	7.7±0.12 (7.5–7.8)	3.9±0.17 (3.7–4.2)	6.2±0.18 (5.9–6.4)	5.5±0.09 (5.5–5.6)
	♀	8	13.8±0.23 (13.6–14.2)	8.8±0.12 (8.6–9.0)	2.8±0.11 (2.6–2.9)	13.0±0.17 (12.9–13.4)	7.7±0.13 (7.6–8.0)	3.9±0.13 (3.8–4.2)	6.1±0.07 (6.0–6.2)	5.6±0.11 (5.4–5.8)
Biliran	♂	2	13.8 (13.5–14.2)	8.8 (8.7–8.9)	2.8 (2.7–2.9)	13.1 (12.9–13.3)	7.7	3.3 (3.2–3.4)	5.9 (5.7–6.1)	5.4 (5.2–5.5)
Maripipi	♂	5	13.4±0.13 (13.3–13.6)	8.6±0.18 (8.4–8.8)	2.9	12.7±0.19 (12.5–13.0)	7.5±0.08 (7.4–7.6)	3.5±0.13 (3.3–3.6)	5.6±0.22 (5.4–6.0)	5.4±0.77 (5.3–5.5)
	♀	7	13.5±0.14 (13.3–13.7)	8.7±0.07 (8.6–8.8)	2.9±0.05 (2.8–2.9)	12.7±0.13 (12.5–12.9)	7.5±0.10 (7.3–7.6)	3.4±0.15 (3.1–3.5)	5.8±0.24 (5.5–6.1)	5.3±0.08 (5.2–5.4)
Taphozous melanopogon										
Leyte	♂	2	20.3 (20.1–20.5)	12.5 (12.4–12.6)	5.8 (5.8–5.9)	19.5 (19.2–19.8)	10.9 (10.8–11.0)	8.0 (8.0–8.1)	—	8.6 (8.5–8.8)
Biliran	♂	4	20.2±0.19 (20.0–20.4)	12.3±0.28 (12.0–12.6)	5.9±0.14 (5.8–6.1)	19.6±0.22 (19.4–19.9)	11.0±0.28 (10.7–11.3)	8.0±0.17 (7.9–8.3)	—	8.6±0.05 (8.6–8.7)
	♀	2	20.3	12.4 (12.3–12.4)	5.8 (5.7–5.8)	19.2 (19.2–19.3)	11.2 (11.1–11.3)	8.2	—	8.7 (8.5–8.8)
Maripipi	♂	1	20.4	12.4	6.1	19.4	11.2	7.4	—	8.5
	♀	5	20.3±0.09 (20.2–20.4)	12.3±0.13 (12.1–12.4)	5.8±0.04 (5.8–5.9)	19.5±0.29 (19.3–20.0)	11.1±0.07 (11.0–11.2)	7.3±0.08 (7.2–7.4)	—	8.7±0.11 (8.5–8.8)
Megaderma spasma										
Leyte	♂	6	23.6±0.52 (23.0–24.4)	15.0±0.37 (14.6–15.6)	3.6±0.10 (3.4–3.7)	22.8±0.52 (22.2–23.6)	11.6±0.27 (11.3–12.1)	5.3±0.17 (5.1–5.7)	7.8±0.31 (7.4–8.3)	9.0±0.14 (8.9–9.2)
	♀	3	23.9 (23.6–24.4)	15.4 (15.2–15.5)	3.5 (3.4–3.7)	23.1 (22.7–23.3)	11.8 (11.7–12.0)	5.5 (5.3–5.7)	7.9 (7.8–7.9)	9.2 (9.0–9.4)
Biliran	♂	1	24.1	15.0	3.5	23.3	11.9	5.4	8.0	9.4

Note: Measurements other than weight are in millimeters.

Leyte or Biliran. Ten females collected on 24 April 1987 were pregnant with single embryos (crown–rump lengths = 18–23 mm). Males and females from Maripipi are of comparable size (table 12) and fall within the size range of a series from Catanduanes (Heaney et al., 1991).

SPECIMENS EXAMINED—Total 17. MARIPIPI: site M12 (17 USNM).

Hipposideros diadema griseus (Meyen, 1833)

The diadem leaf-nosed bat is widespread from southern Asia to northern Australia. It occurs throughout the Philippines in a variety of habitats ranging from agricultural situations to primary forest. On Leyte, this was the most common microchiropteran captured in second growth forest at 50 m (site L2). We also netted specimens in primary lowland forest at 500 m (site L4; table 10). We did not encounter this species on Biliran or Maripipi. A pregnant female carrying a single embryo (crown–rump length = 15 mm) was collected on 28 March 1987. Cranial measurements for a large series of Leyte males (table 12) are substantially greater than those for three males from Catanduanes (Heaney et al., 1991).

SPECIMENS EXAMINED—Total 47. LEYTE: Leyte Prov.: site L2 (6 USNM); site L4 (1 UMMZ, 2 USNM); site L14 (26 AMNH, 12 DMNH).

Hipposideros obscurus (Peters, 1861)

This leaf-nosed bat is a Philippine endemic, with previous records from Catanduanes, Dinagat, Luzon, and Mindanao (Heaney et al., 1991). On Ma-

TABLE 11. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
4.1±0.05	3.4±0.13	5.8±0.15	63±3.3	11±1.0	9±0.5	15±1.3	46±1.1	5.8±0.27
(4.0–4.1)	(3.2–3.5)	(6.4–6.8)	(59–66)	(9–12)	(8–10)	(12–16)	(44–47)	(5.5–6.0)
4.2±0.07	3.3±0.11	5.8±0.19	66±1.6	12±0.5	9	16±0.5	46±0.8	6.1±0.18
(4.1–4.3)	(3.2–3.5)	(5.4–6.0)	(64–69)	(11–12)		(15–16)	(45–47)	(6.0–6.5)
4.1	3.3	5.5	62	10	10	15	45	5.0
	(3.2–3.4)	(5.1–5.9)	(62–63)	(10–11)	(9–10)			
4.0±0.04	3.2±0.10	5.6±0.19	58±1.0	10±0.7	8±0.6	14±0.6	45±2.2	5.1±0.65
(3.9–4.0)	(3.1–3.3)	(5.4–5.9)	(57–59)	(9–11)	(7–8)	(14–15)	(44–49)	(4.2–6.0)
4.0±0.09	3.2±0.10	5.7±0.10	59±2.9	11±1.0	8±0.8	14±1.2	45±1.0	5.4±0.37
(3.9–4.1)	(3.0–3.3)	(5.5–5.7)	(56–62)	(9–12)	(7–9)	(12–16)	(44–47)	(5.0–6.0)
6.0	5.2	5.8	106	23	12	22	64	23
(6.0–6.1)	(5.2–5.3)	(5.5–6.0)	(104–107)	(22–24)			(63–64)	
6.0	5.0±0.26	6.0±0.17	105±2.4	21±0.8	13±1.0	22±1.0	63±1.0	24±1.3
	(4.7–5.3)	(5.8–6.2)	(102–107)	(20–22)	(12–14)	(20–22)	(62–64)	(22–25)
6.2	5.0	5.9	105	21	13	22	64	26
(6.1–6.3)	(6.1–6.3)	(4.9–5.0)	(103–107)	(20–22)		(20–23)	(63–64)	(24–28)
5.8	5.2	5.9	100	20	13	24	63	22.5
5.9±0.05	5.1±0.11	5.9±0.14	102±1.7	22±1.6	13±0.4	23±0.5	64±0.9	27.0±1.58
(5.9–6.0)	(5.0–5.3)	(5.7–6.0)	(100–104)	(21–25)	(13–14)	(22–23)	(62–64)	(26.3–29.0)
7.0±0.16	3.9±0.10	6.6±0.16	80±4.9	0	20±1.1	41±1.0	60±1.7	24±2.3
(6.8–7.2)	(3.8–4.0)	(6.4–6.8)	(75–86)		(19–22)	(40–42)	(58–62)	(21–27)
7.0	3.9	6.8	84	0	20	42	61	28
(6.9–7.2)	(3.7–4.1)	(6.6–6.9)	(82–89)		(20–21)	(41–43)	(60–62)	(26–31)
7.2	3.9	7.3	80	0	21	36	62	26

ripipi, we captured them in disturbed lowland forest at 600 m and primary mossy forest at 740 m (sites M2 and M4; table 10). None were encountered on Leyte or Biliran. Three females taken during the third week of April 1987 were pregnant with single embryos (crown–rump lengths = 5–7 mm). Males of this species are consistently larger than females in most cranial dimensions (table 12). Maripipi specimens are substantially smaller than two individuals from Catanduanes (Heaney et al., 1991).

SPECIMENS EXAMINED—Total 5. MARIPIPI: site M2 (1 UMMZ); site M4 (4 USNM).

Rhinolophus arcuatus Peters, 1871

This species occurs from Sumatra to New Guinea. In the Philippines, there appear to be two species, differing mostly in body size, that are currently included under this name (Heaney et al., 1991; Ingle & Heaney, 1992). Specimens reported here match the smaller species more closely (table 12; table 2 in Heaney et al., 1991). We captured two specimens in primary forest at 500 m on Leyte (site L4; table 10). On Biliran, this was the second most commonly taken microchiropteran. We netted one specimen in secondary forest at 450 m (site B1) and five in primary montane forest at 850 m elevation (site B3; table 10). On Maripipi, two specimens were netted in primary mossy forest at 700 m (site M4; table 10). Females pregnant with single embryos (crown–rump lengths = 10–17 mm) were taken between 2 and 26 April.

SPECIMENS EXAMINED—Total 11. LEYTE: Leyte Prov.: site L4 (2 USNM); site L14 (1 DMNH). BILIRAN: site B1 (1 USNM); site B3 (5 USNM). MARIPIPI: site M4 (2 USNM).

TABLE 12. Means (± SD) and ranges of selected measurements of adult bats (Rhinolophidae) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-incisive length	Zygomatic breadth	Inter-orbital width	Condylo-canine length	Mastoid breadth	Rostral length	Orbital length	C to last M
Hipposideros ater										
Maripipi	♂	4	14.3±0.17 (14.1–14.5)	7.9±0.18 (7.7–8.1)	2.4±0.08 (2.3–2.5)	13.3±0.10 (13.2–13.4)	8.4±0.14 (8.3–8.6)	4.4±0.13 (4.3–4.6)	4.8±0.14 (4.6–4.9)	4.8±0.24 (4.5–5.0)
	♀	6	14.3±0.20 (14.0–14.6)	7.8±0.14 (7.6–8.0)	2.3±0.13 (2.1–2.5)	13.2±0.19 (12.9–13.4)	8.5±0.10 (8.4–8.7)	4.3±0.13 (4.1–4.5)	4.7±0.31 (4.3–5.1)	4.7±0.08 (4.6–4.8)
Hipposideros diadema										
Leyte	♂	11	29.2±0.46 (28.5–29.9)	18.2±0.39 (17.7–19.0)	3.3±0.28 (2.8–3.8)	27.3±0.90 (26.5–29.9)	14.8±0.29 (14.3–15.2)	10.5±0.22 (10.1–10.9)	10.3±0.35 (9.6–10.9)	11.8±0.18 (11.4–12.0)
Hipposideros obscurus										
Maripipi	♂	2	16.4 (16.3–16.5)	10.6	2.5	15.2 (14.8–15.6)	9.4	5.0 (4.8–5.1)	6.7 (6.6–6.8)	6.0 (5.8–6.1)
	♀	2	15.8	10.4 (10.2–10.5)	2.4 (2.3–2.5)	15.0 (14.8–15.2)	9.1	4.7	6.4 (6.2–6.5)	6.0 (5.9–6.2)
Rhinolophus arcuatus										
Leyte	♂	1	18.6	9.4	2.0	17.4	9.6	8.4	5.3	7.5
	♀	1	18.4	9.3	1.8	16.8	9.4	7.8	5.5	7.3
Biliran	♂	1	—	8.8	1.9	16.3	9.1	—	4.8	6.7
	♀	2	17.6 (17.5–17.6)	8.8	1.9	16.2	9.0	7.6	4.9 (4.8–5.0)	6.8 (6.7–6.9)
Maripipi	♀	1	19.0	9.5	1.9	17.4	9.6	8.1	5.3	7.4
Rhinolophus inops										
Leyte	♂	12	22.4±0.26 (22.0–22.8)	11.5±0.14 (11.3–11.7)	2.1±0.15 (1.9–2.4)	20.4±0.17 (20.2–20.8)	11.0±0.12 (10.8–11.2)	9.7±0.18 (9.4–10.0)	6.2±0.16 (5.9–6.5)	8.9±0.13 (8.7–9.1)
	♀	9	22.0±0.29 (21.7–22.5)	11.3±0.22 (11.0–11.6)	2.0±0.07 (1.9–2.1)	20.3±0.20 (20.1–20.7)	10.8±0.12 (10.6–10.9)	9.6±0.21 (9.4–10.0)	6.2±0.15 (6.0–6.4)	8.8±0.14 (8.6–9.1)
Biliran	♂	7	22.5±0.35 (21.8–22.9)	11.6±0.16 (11.3–11.7)	2.1±0.14 (1.9–2.3)	20.7±0.36 (19.9–21.0)	11.0±0.21 (10.7–11.3)	9.9±0.16 (9.7–10.1)	6.4±0.15 (6.2–6.5)	9.0±0.18 (8.7–9.2)
	♀	11	22.3±0.21 (21.9–22.6)	11.4±0.22 (11.0–11.8)	2.0±0.20 (1.7–2.3)	20.3±0.13 (20.1–20.5)	11.0±0.20 (10.7–11.4)	9.7±0.15 (9.5–9.9)	6.3±0.22 (6.1–6.8)	8.7±0.21 (8.3–8.9)
Rhinolophus rufus										
Leyte	♂	1	27.3	14.1	2.7	25.4	12.8	11.6	7.9	11.0
Rhinolophus virgo										
Leyte	♂	1	16.7	8.0	2.3	15.2	8.6	7.1	4.2	6.2
	♀	1	—	8.3	2.3	14.4	8.0	—	4.4	5.9
Maripipi	♀	1	15.6	8.7	2.4	14.2	8.2	6.6	4.3	5.8

Note: Measurements other than weight are in millimeters.
* Measured from dry skin.

Rhinolophus inops K. Andersen, 1905

This horseshoe bat is a Philippines endemic. Previous records are from Catanduanes, Leyte, Luzon, Mindanao, Mindoro, and Negros (Heaney et al., 1991). It was by far the most common microchiropteran species that we encountered at primary forest sites on both Leyte and Biliran (table 10). On Mt. Pangasugan, Leyte, it was abundant in lowland forest at 500 m (site L4), common in montane forest at 700 m and ridgetop mossy forest at 950 m (sites L5 and L6), and rare in secondary forest at 50 m (site L2). Specimens have also been taken at Paril Cave on Leyte (site L14). On Biliran, it was very abundant in primary montane forest at 850 m elevation (site B3) and less common in forest plantation and adjacent agricultural situations at 400 m (site B1). In marked contrast to the pattern on Leyte and Biliran, the species was not recorded on Maripipi despite considerable netting effort (65 net-nights) in suitable forested habitats. Females pregnant with single embryos (crown–

TABLE 12. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
3.8±0.29	3.2±0.10	4.8±0.13	75±3.6	30±2.5	8±0.6	19	40±0.6	5.5±0.65
(3.6–4.2)	(3.1–3.3)	(4.7–5.0)	(71–79)	(27–33)	(7–8)		(39–40)	(5.2–6.5)
4.0±0.16	3.3±0.13	5.0±0.10	75±2.6	30±1.0	7	19±0.8	40±0.8	5.9±0.85
(3.7–4.2)	(3.2–3.5)	(4.8–5.1)	(71–78)	(29–32)		(18–20)	(39–41)	(5.0–6.7)
8.9±0.29	8.0±0.34	11.4±0.29	148±3.8	48±4.7	19±1.3	32±1.0	84±1.0	43±6.0
(8.4–9.4)	(7.4–8.6)	(11.0–11.9)	(144–151)	(43–54)	(17–20)	(31–33)	(83–85)	(39–52)
5.0	5.1	5.8	71	22	10	20	44	8.3
(4.9–5.1)		(5.7–5.8)	(67–75)	(20–23)	(10–11)		(44–45)	
5.2	5.0	5.7	71	21	10	20	44	7.4
(5.1–5.3)	(4.9–5.0)					(19–20)	(43–45)	(7.0–7.8)
5.4	3.9	5.8	–	–	–	–	–	–
5.4	4.1	6.3	70	20	10	21	45	8
4.8	3.9	–	70	22	11	22	43	7
5.0	3.8	5.8	71	21	11	20	44	8
(4.9–5.1)	(3.7–3.8)	(5.8–5.9)	(69–73)		(10–12)	(20–21)	(43–44)	(7–8)
5.5	4.0	6.4	68	16	9	21	45	8.7
6.5±0.16	4.8±0.14	8.0±0.23	84±5.3	22±1.7	13±1.4	26±1.6	52±0.7	13±1.1
(6.2–6.8)	(4.6–5.1)	(7.5–8.2)	(78–92)	(15–24)	(11–15)	(23–27)	(51–53)	(12–15)
6.5±0.10	4.8±0.17	7.6±0.12	83±6.4	23±2.2	13±1.0	25±2.4	53±0.9	13±1.5
(6.4–6.7)	(4.5–5.1)	(7.5–7.8)	(73–94)	(21–28)	(12–15)	(21–27)	(52–54)	(11–15)
6.6±0.09	4.8±0.14	7.9±0.21	85±1.2	24±2.0	14±1.0	27±0.7	53±1.3	14±1.0
(6.5–6.7)	(4.6–5.0)	(7.7–8.2)	(83–87)	(21–27)	(13–15)	(26–28)	(51–55)	(12–15)
6.6±0.16	4.8±0.14	7.8±0.23	87±2.6	24±1.7	14±0.6	27±0.5	52±0.8	15±0.8
(6.4–7.0)	(4.6–5.0)	(7.3–8.0)	(80–90)	(20–26)	(13–15)	(26–27)	(50–53)	(14–16)
8.2	6.4	9.2	–	–	–	–	67.5*	–
4.9	3.4	5.9	70	24	8	21	42	5.5
4.4	3.4	–	71	26	9	17	41	5.5
4.4	3.5	5.5	67	24	8	18	40	6.5

rump lengths = 8–18 mm) were taken between 23 March and 27 April 1987. Males of this species are slightly larger than females in most cranial dimensions (table 12). Specimens from Leyte and Biliran are not distinguishable and are similar in size to specimens from Catanduanes (Heaney et al., 1991); those from Negros are distinctly smaller (Ingle & Heaney, 1992).

SPECIMENS EXAMINED—Total 88. LEYTE: Leyte Prov.: site L2 (1 USNM); site L4 (2 SU, 25 USNM); site L5 (6 USNM); site L6 (6 USNM); site L14 (5 DMNH). BILIRAN: site B1 (9 USNM); site B3 (2 PNM, 30 USNM, 2 WAM).

Rhinolophus rufus Eydoux & Gervais, 1836

This species is a Philippine endemic, with prior records from Bohol, Catanduanes, Luzon, Mindanao, and Mindoro (Heaney et al., 1991). We captured none, but in 1963 specimens were col-

TABLE 13. Means (± SD) and ranges of selected measurements of adult vespertilionid bats (*Harpiocephalus, Kerivoula,* and *Miniopterus*) from Leyte and Biliran islands.

	Sex	N	Condylo-incisive length	Zygomatic breadth	Inter-orbital width	Condylo-canine length	Mastoid breadth	Rostral length	Orbital length	C to last M
Harpiocephalus harpia										
Leyte	♂	1	20.6	14.7	5.9	19.7	12.0	5.4	7.8	6.9
Kerivoula hardwickii										
Leyte	♂	1	12.6	8.9	3.4	12.1	7.6	3.1	4.1	5.1
Biliran	♂	1	12.7	8.9	3.3	11.9	7.6	3.1	4.0	5.1
Miniopterus australis										
Leyte	♂	1	13.4	7.4	3.3	12.5	7.5	4.2	4.4	5.3
	♀	1	13.2	7.6	3.3	12.3	7.5	4.2	4.0	5.3
Miniopterus schreibersii										
Leyte	♂	4	15.0±0.03 (14.6–15.3)	8.8±0.13 (8.6–8.9)	3.8±0.08 (3.7–3.9)	13.8±0.25 (13.5–14.0)	8.6±0.10 (8.5–8.7)	4.4±0.12 (4.3–4.5)	5.1±0.15 (4.9–5.2)	6.1±0.05 (6.0–6.1)
	♀	6	15.1±0.18 (14.9–15.4)	8.7±0.12 (8.5–8.8)	3.7±0.10 (3.6–3.8)	14.0±0.15 (13.8–14.2)	8.4±0.16 (8.2–8.6)	4.4±0.1 (4.3–4.6)	5.2±0.14 (5.0–5.3)	6.2±0.08 (6.1–6.3)
Miniopterus tristis										
Leyte	♂	1	18.8	11.0	4.0	17.4	10.1	5.4	6.8	8.0
	?	1	18.2	10.3	4.0	16.7	9.7	5.0	6.5	7.7

Note: Measurements other than weight are in millimeters.

lected at Paril Cave on Leyte (site L14). One of these, an adult male, is similar in size to a specimen from Catanduanes (table 11; Heaney et al., 1991).

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L14 (2 DMNH).

Rhinolophus virgo K. Andersen, 1905

We obtained four specimens of this widespread Philippine endemic in primary lowland forest at 500 m on Leyte (site L4; table 12). On Maripipi, we netted one specimen in primary mossy forest at 740 m (site M4; table 10). Pregnant females taken between 30 March and 21 April contained single embryos (crown–rump lengths = 8–15 mm). Measurements for our series (table 12) are comparable to those for a single specimen from Catanduanes (Heaney et al., 1991).

SPECIMENS EXAMINED—Total 5. LEYTE: Leyte Prov.: site L4 (4 USNM). MARIPIPI: site M4 (1 USNM).

Family **Vespertilionidae**—Common Bats

Harpiocephalus harpia (Temminck, 1840)

We netted a single specimen of the hairy winged bat in primary lowland dipterocarp forest at 500 m elevation on Mt. Pangasugan, Leyte (site L4; table 10). Other Philippine island records for this widespread Asian species (Koopman, 1989) include Luzon (Ingle & Heaney, 1992) and Negros (Utzurrum, unpubl. data). Measurements are given in Table 13.

SPECIMENS EXAMINED—Total 1. LEYTE: Leyte Prov.: site L4 (1 USNM).

Kerivoula hardwickii (Horsfield, 1825)

We netted two woolly bats on Mt. Pangasugan, one in primary dipterocarp forest at 500 m and another in ridgetop mossy forest at 950 m (sites L4 and L6; table 10). Other Philippine records for this widespread Asian species are from Mindanao, Palawan, and Samar. Table 13 contains measurements for our specimens.

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L4 (1 USNM); site L6 (1 USNM).

Miniopterus australis paululus Hollister, 1913

The lesser bent-winged bat occurs from India to Australia and is found throughout the Philippines. Some authors treat *paululus* as a distinct

TABLE 13. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
5.0	4.8	9.1	125	46	14	18	51	19
3.4	2.8	5.0	86	43	9	14	35	4
3.4	2.8	5.1	77	38	10	15	34	4.5
3.9	2.8	6.1	87	36	7	9	36	4
3.8	3.0	5.6	91	41	7	11	37	5
4.4±0.05	3.6±0.10	6.5±0.10	108±3.7	49±3.3	10±0.6	12±1.0	44±0.5	10±0.5
(4.3–4.4)	(3.4–3.6)	(6.4–6.6)	(103–112)	(47–54)	(9–10)	(11–13)	(43–44)	(9–10)
4.5±0.08	3.4±0.14	6.6±0.15	107±3.7	48±1.8	9	12±1.0	44±1.2	10±2.6
(4.4–4.6)	(3.2–3.6)	(6.4–6.8)	(102–113)	(46–51)		(11–13)	(43–46)	(8–14)
6.0	4.5	8.3	132	59	11	15	54	18
5.6	4.3	8.1	–	–	–	–	51	–

species (Hill, 1983; Koopman, 1989). This species and other species of bent-winged bats depend on caves for roost sites. On Leyte, we found a few *M. australis* roosting in several small solution cavities in one of the darkest parts of Cathedral Cave (site L7). None were encountered on Biliran or Maripipi. One female specimen taken on 19 March contained a single embryo (crown–rump length = 6 mm). Cranial measurements of two Leyte specimens are consistently larger than those for a series from Catanduanes (table 13; Heaney et al., 1991).

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L7 (2 USNM).

Miniopterus schreibersii eschscholtzii Waterhouse, 1845

This species of bent-winged bat is very widespread, occurring in Europe, Africa, Asia, and Australia. It is found throughout the Philippines. This species was moderately common in the second largest of the Cathedral caves on Leyte (site L7). We also netted four specimens in primary lowland forest at 500 m on Mt. Pangasugan and one in montane forest at 700 m (sites L4 and L5; table 10). None were taken on Biliran or Maripipi. Females pregnant with single embryos (crown–rump lengths = 4–9 mm) were taken during March. Cranial and forearm measurements of Leyte specimens (table 13) are similar to those for a series from Catanduanes (Heaney et al., 1991).

SPECIMENS EXAMINED—Total 26. LEYTE: Leyte Prov.: site L4 (4 UMMZ, 2 USNM); site L5 (1 USNM); site L7 (15 UMMZ, 4 USNM).

Miniopterus tristis tristis (Waterhouse, 1845)

This species is found from the Philippines to the Solomon Islands. It occurs throughout the Philippines with the possible exception of the Palawan faunal region. On Leyte, we netted one specimen in disturbed lowland forest at 50 m (site L2; table 10). Another was found dead on the floor of Cathedral Cave (site L7). The species was not recorded on either Biliran or Maripipi. Measurements are given in Table 13.

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L2 (1 USNM); site L7 (1 UMMZ).

Murina cyclotis Dobson, 1872

This species of tube-nosed bat occurs throughout southern Asia. Previous Philippine records (all based on single specimens) are from Luzon, Mindanao, and Catanduanes (Heaney et al., 1991). We

TABLE 14. Means (± SD) and ranges of selected measurements of adult vespertilionid bats (*Murina, Myotis, Philetor,* and *Scotophilus*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Condylo-incisive length	Zygomatic breadth	Inter-orbital width	Condylo-canine length	Mastoid breadth	Rostral length	Orbital length	C to last M
Murina cyclotis										
Biliran	♀	1	16.7	10.7	4.7	—	8.7	—	6.3	5.9
Myotis muricola										
Leyte	♂	2	12.0 (11.9–12.2)	8.0	3.1	11.3 (11.1–11.5)	6.8 (6.7–6.9)	3.6	4.3 (4.2–4.4)	4.8 (4.7–4.8)
	♀	1	12.2	8.0	3.1	11.3	6.8	3.4	4.4	4.8
Biliran	♂	1	12.1	7.8	2.9	11.4	6.6	3.4	4.2	4.7
	♀	4	12.0±0.08 (11.9–12.1)	7.7±0.13 (7.6–7.9)	3.0±0.13 (2.9–3.2)	11.2±0.06 (11.1–11.2)	6.6±0.18 (6.4–6.8)	3.8	4.1±0.21 (3.9–4.3)	4.7±0.05 (4.7–4.8)
Maripipi	♀	1	12.3	7.5	2.9	11.5	6.5	3.7	4.1	4.8
Philetor brachypterus										
Leyte	♂	2	13.6 (13.1–14.0)	10.2 (9.9–10.4)	4.9	12.9 (12.5–13.3)	8.6 (8.4–8.9)	3.7 (3.5–3.9)	5.3 (5.2–5.4)	4.6 (4.4–4.8)
Scotophilus kuhlii										
Leyte	♂	12	18.0±0.38 (17.6–18.7)	13.2±0.30 (12.8–13.8)	4.7±0.27 (4.6–5.6)	17.2±0.35 (16.7–17.8)	11.2±0.26 (10.8–11.6)	4.1±0.17 (3.8–4.4)	7.4±0.22 (7.1–7.7)	6.5±0.19 (6.2–6.9)
	♀	10	18.0±0.19 (17.6–18.2)	13.2±0.17 (12.8–13.4)	4.7±0.08 (4.6–4.8)	17.1±0.30 (16.8–17.6)	11.3±0.19 (11.0–11.6)	4.1±0.13 (3.9–4.3)	7.4±0.23 (6.9–7.8)	6.5±0.11 (6.4–6.7)
Biliran	♂	3	17.9 (17.7–18.0)	12.8 (12.7–12.9)	4.5 (4.4–4.6)	17.0 (16.8–17.2)	10.9 (10.7–11.0)	4.0 (3.8–4.1)	7.3 (7.2–7.3)	6.5 (6.4–6.6)
	♀	3	17.7 (17.4–18.1)	12.9 (12.9–13.0)	4.5 (4.4–4.6)	16.9 (16.6–17.2)	11.0 (10.8–11.3)	4.2 (4.1–4.3)	7.3 (7.2–7.4)	6.4 (6.2–6.6)

Note: Measurements other than weight are in millimeters.

netted a single female on Biliran in partially logged primary forest at 700 m elevation (site B2; table 10). None were taken on Leyte or Maripipi. Measurements for the Biliran specimen are comparable to those for a male from Catanduanes (table 14; Heaney et al., 1991).

SPECIMENS EXAMINED—Total 1. BILIRAN: site B2 (1 UMMZ).

Myotis muricola browni Taylor, 1934

This species is widespread in southern Asia and occurs throughout the Philippines (Hill, 1983; Koopman, 1989). On Leyte, we netted two specimens in disturbed lowland forest at 50 m and another in primary forest at 500 m (sites L2 and L4; table 10). Specimens from Biliran were taken in forest plantation at 50 m (site B1), in partially logged primary lowland forest at 700 m (site B2), and in primary montane forest at 850 m (site B3; table 10). A single specimen from Maripipi was netted over a stream in the village of Viga (site M5). Two lactating females were captured in late April. Table 14 contains measurements for our specimens.

SPECIMENS EXAMINED—Total 9. LEYTE: Leyte Prov.: site L2 (2 USNM); site L4 (1 UMMZ). BILIRAN: site B1 (1 USNM); site B2 (3 UMMZ); site B3 (1 USNM). MARIPIPI: site M5 (1 USNM).

Philetor brachypterus (Temminck, 1840)

This bat occurs from Nepal to New Guinea. Previous Philippine records are from Mindanao and Negros. On Leyte, we netted two specimens in primary lowland forest at 500 m elevation (site L4; table 10). The species was not encountered on either Biliran or Maripipi. Measurements appear in Table 14.

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L4 (2 USNM).

TABLE 14. *Extended.*

Molariform toothrow	Palatal breadth at last M	Palatal length	Total length	Tail length	Hindfoot	Ear	Forearm	Weight (g)
4.7	3.8	7.4	98	38	9	15	36	10
3.4 (3.4–3.5)	3.0 (2.9–3.0)	5.6 (5.5–5.8)	75 (74–76)	32 (30–33)	6 (6–7)	12 (12–13)	30 (30–31)	3.8 (3.5–4.0)
3.4	3.2	5.2	79	35	7	14	31	3.5
3.4	2.9	5.3	69	30	8	12	32	3.5
3.5±0.08 (3.4–3.6)	2.8±0.08 (2.7–2.9)	5.2±0.14 (5.1–5.4)	76±2.4 (73–79)	32±0.5 (32–33)	7±0.8 (6–8)	12±0.5 (12–13)	32±1.5 (31–34)	4.0
3.6	2.8	5.6	73	31	7	12	31	3.8
3.6 (3.6–3.7)	4.0 (3.9–4.1)	5.0 (4.4–5.5)	94 (90–99)	34 (32–37)	10 (9–10)	14	36 (35–36)	9.8 (8.5–11.0)
5.3±0.15 (5.1–5.5)	5.0±0.15 (4.8–5.3)	7.0±0.23 (6.5–7.3)	117±7.8 (104–127)	46±4.6 (36–50)	12±0.7 (11–13)	14±0.4 (14–15)	50±1.2 (48–52)	19±0.9 (18–20)
5.3±0.14 (5.1–5.5)	5.2±0.13 (5.0–5.4)	7.0±0.25 (6.6–7.3)	121±3.0 (117–126)	45±2.8 (41–49)	12±0.5 (11–13)	15±0.7 (14–16)	50±0.8 (48–50)	20±1.5 (18–22)
5.3 (5.2–5.4)	5.1 (5.0–5.3)	6.9 (6.8–7.2)	118 (117–118)	47 (44–52)	12	15	49 (48–50)	17
5.2 (5.0–5.4)	5.0 (4.8–5.2)	6.8 (6.6–7.0)	120 (114–124)	44 (40–47)	13	15	50 (48–53)	18.0 (17–19)

Scotophilus kuhlii Leach, 1822

The widespread Asian house bat is abundant in most urban and agricultural areas throughout the Philippines. Our observations indicate that it is rare in forested habitats. On Leyte, it was abundant in the lowlands around the campus of the Visayas State College of Agriculture (site L1), where specimens were collected from a roost of several hundred in the attic of a large building. Five others were netted along a stream in secondary forest at 50 m elevation at the base of Mt. Pangasugan (site L2; table 10). On Biliran, we netted house bats and collected them from roosts in buildings in the town of Naval (site B5). Here they were also seen roosting under the dead fronds of an ornamental fan palm, *Livistona rotundifolia*. Some of the fronds may have been modified to form "tents"; *S. kuhlii* is the only vespertilionid known to exhibit this behavior (Rickart et al., 1989b). On Maripipi, one specimen was netted at 400 m elevation on a ridge between areas of secondary lowland forest (site M1; table 10), and six others were netted over a stream in the village of Viga (site M5). Females collected during April all contained two embryos. Pregnancies among a series of 14 females taken from a single colony on 27 April were relatively asynchronous (crown–rump lengths = 7–21 mm). Specimens from Leyte have slightly larger crania than do those from Biliran (table 14).

SPECIMENS EXAMINED—Total 89. LEYTE: Leyte Prov.: site L1 (13 USNM); site L2 (5 USNM); site L15 (15 AMNH); site L16 (22 FMNH). BILIRAN: site B5 (2 PNM, 1 SU, 9 UMMZ, 14 USNM, 1 VISCA). MARIPIPI: site M1 (1 UMMZ); site M5 (6 USNM).

OTHER RECORDS—LEYTE: site L17 (ROM).

Family **Molossidae**—Free-Tailed Bats

Chaerephon plicata (Buchanon, 1800)

This species of free-tailed bat is found from India to Southeast Asia. *Chaerephon*, formerly a sub-

TABLE 15. Means (± SD) and ranges of selected measurements of adult *Tarsius syrichta* from Leyte Island.

	Sex	N	Condylo-basal length	Greatest length of skull	Zygomatic (post-orbital) breadth	Braincase breadth	Orbital breadth	Inter-orbital breadth	Rostral length	First incisor to third molar
Leyte	♂	2	31.9 (31.0–32.8)	40.0 (39.3–40.6)	27.9 (27.6–28.2)	22.5 (22.1–22.9)	32.2 (31.9–32.5)	1.7	7.3 (7.2–7.4)	17.0 (16.8–17.1)

Note: Measurements other than weight are in millimeters.

genus of *Tadarida,* was recognized as a valid genus by Freeman (1981). *Chaerephon plicata* is widespread in the Philippines, with records from Cebu, Leyte, Luzon, Mindanao, and Negros. There are no records from either Biliran or Maripipi. This bat apparently depends on caves for roosting sites. The only specimens known from Leyte are a series collected at Cathedral Cave (site L7) by D. Empesso in 1963. The species was not encountered during our extensive investigations of the Cathedral Cave complex in 1984 and 1987. We suspect that the colony has been extirpated.

SPECIMENS EXAMINED—None.

OTHER RECORDS—LEYTE: Leyte Prov.: site L7 (54 ROM).

Order **Primates**
Family **Tarsiidae**—Tarsiers

Tarsius syrichta (Linnaeus, 1758)

The Philippine tarsier is restricted to the Mindanao faunal region (see map in Musser & Dagosto, 1987). On Leyte, we encountered it in mixed secondary forest and agricultural land between 50 and 100 m elevation (site L2) and in primary lowland and montane forest between 300 and 700 m (sites L3–L5). We obtained no specimens on either Biliran or Maripipi. However, we received persistent reports of tarsiers and believe that they are present on both of the smaller islands. According to farmers and hunters on Leyte, tarsiers are common at low elevations and are often seen in pairs. They are strictly nocturnal and are excellent climbers and jumpers. On Mt. Pangasugan, we captured two individuals in mist nets set ca. 1–2 m above the forest floor. A female taken on 31 March contained a single embryo (crown–rump length = 13 mm). Two males from Leyte (table 15) fall within the size range of a series from Mindanao but are substantially smaller than a male from Dinagat (Heaney & Rabor, 1982).

SPECIMENS EXAMINED—Total 9. LEYTE: Leyte Prov.: site L2 (1 PNM, 1 UMMZ, 2 VISCA); site L3 (1 USNM); site L4 (2 USNM); Site L5 (1 PNM); site L15 (1 AMNH).

OTHER RECORDS—LEYTE: site L21 (Taylor, 1934).

Family **Cercopithecidae**—Monkeys

Macaca fascicularis philippinensis Geoffroy, 1843

The long-tailed macaque occurs from Burma to Timor and is found throughout the Philippines. Fooden (1991) has shown that specimens from Leyte belong to the endemic Philippine subspecies *philippinensis.* On Leyte, the species was relatively common in the Mt. Pangasugan region, where they were observed in lowland and montane forest habitats between 50 and 700 m (sites L2–L5). We received specimens from local hunters that had been obtained from near 500 m (site L4) and from unknown elevations. Monkeys were also reportedly common on both Biliran and Maripipi, where we sighted small troops of 5–10 individuals in primary forest between 800 and 850 m elevation (site B3) and at 650 m (site M4). We also obtained two fresh specimens from hunters on Maripipi and old specimens from local hunters on both islands. According to farmers and hunters in the Mt. Pangasugan region, monkeys occur at all elevations but are most common in lowland forest. They eat a wide variety of fruits and frequently raid crops during periods when wild foods are scarce. They are heavily hunted by local peoples both as agricultural pests and as a source of meat. Cranial measurements of males from Leyte and Biliran are given in Table 16.

SPECIMENS EXAMINED—Total 22. LEYTE: Leyte Prov.: site L4 (1 UMMZ); vicinity of Mt. Pangasugan (2 USNM); site L15 (3 AMNH); site L10 (2 AMNH). BILIRAN: no specific locality (1 USNM).

TABLE 15. *Extended.*

First molar to third molar	Labial width at second molars	Palatal width at third molars	Total length	Tail length	Hindfoot	Weight (g)
7.5 (7.4–7.6)	4.2 (4.1–4.4)	9.2 (8.6–9.7)	354 (350–357)	238 (230–245)	62 (60–65)	123

MARIPIPI: site M7 (1 USNM); site M10 (1 UMMZ); no specific locality (4 UMMZ, 7 USNM).

SPECIMENS EXAMINED—Total 5. LEYTE: Leyte Prov.: site L8 (3 DMNH); site L11 (1 DMNH). BILIRAN: site B1 (1 USNM).

Order **Rodentia**
Family **Sciuridae**—Squirrels

Exilisciurus concinnus (Thomas, 1888)

The Philippine pygmy squirrel is endemic to the Mindanao faunal region. Animals from Leyte, Samar, and adjacent small islands previously were known under the name *E. samaricus* but are now regarded as indistinguishable from the Mindanao form (Heaney, 1985a). Pygmy squirrels are apparently restricted to primary and secondary forest habitats, mostly at elevations above 500 m (Heaney, 1985a). Specimens have been taken at Buri and on Bulog Peak on Leyte (sites L8 and L11). On Biliran, we collected single specimens in disturbed lowland and montane forest at 450 and 800 m elevation (sites B1 and B3). Both of these were shot in the early morning as they foraged in trees on the margins of forest clearings. One was taken before dawn when it was still dark. Other individuals were seen on the ground and on tree trunks in areas of recent selective logging in primary forest on Biliran at 700, 800, and 920 m elevation. Pygmy squirrels were not observed on Maripipi, where local informants had no knowledge of them. Measurements for Leyte specimens fall within the range of variation observed among specimens from Dinagat, Siargao, and Mindanao (table 17; Heaney, 1985a; Heaney & Rabor, 1982).

Sundasciurus samarensis (Steere, 1890)

The type locality of this squirrel was given by Steere (1890) as "Samar and Leyte"; it also occurs on Bohol and may prove to be a subspecies of *S. philippinensis* (Heaney et al., 1987). On Mt. Pangasugan, tree squirrels were common in disturbed forest and adjacent upland agricultural land below 200 m. They were also observed in primary lowland and montane forest up to 700 m. On Biliran, four animals were shot in a partially logged clearing in primary montane forest at 800 m (site B3), and another was shot from a tree in an area of recent logging in montane forest at 920 m (site B4). Two others were collected in a patch of remnant lowland forest at 400 m (site B1). The species was not encountered on Maripipi, and according to local farmers they do not occur on the island. Squirrels apparently are most common in primary and secondary forest at low and mid-elevations. In agricultural areas near forest they reportedly damage corn and sweet potatoes and, consequently, are hunted as pests. A series of specimens taken between 5 and 7 April 1987 included a lactating female with four placental scars, a female with a fresh vaginal copulatory plug, and several males in breeding condition (scrotal testes, from 7 × 13 to 12 × 20 mm). External measurements of males average slightly larger than those of females; how-

TABLE 16. Selected cranial measurements of adult *Macaca fascicularis* from Leyte and Biliran islands.

	Sex	N	Zygomatic breadth	Interorbital width	Postorbital width	Mastoid breadth	Orbital length	C to last M	Molariform toothrow	Palatal breadth at last M	Palatal length
Leyte	♂	1	83.9	6.0	41.5	69.2	22.7	41.6	31.2	21.7	54.8
Biliran	♂	1	82.2	6.1	41.8	66.5	22.5	39.9	29.8	—	53.6

Note: Measurements are in millimeters.

TABLE 17. Means (± SD) and ranges of selected measurements of adult sciurid rodents from Leyte and Biliran islands.

	Sex	N	Basioccipital length	Interorbital width	Zygomatic breadth	Mastoid breadth	Nasal length	Anterior nasal breadth	Rostral depth	Rostral length
Exilisciurus concinnus										
Leyte	♂	3	22.9	10.8 (10.6–11.0)	—	11.9	7.7 (7.6–7.7)	3.4 (3.2–3.6)	5.4 (5.3–5.4)	12.8 (12.7–13.0)
Biliran*		1								
Sundasciurus samarensis										
Leyte	♂	22	45.1±0.85 (43.5–46.6)	16.7±0.54 (15.6–17.7)	29.2±0.69 (27.9–31.2)	21.3±0.43 (20.7–22.0)	15.4±0.47 (14.7–16.4)	6.7±0.37 (6.1–7.5)	10.3±0.41 (9.3–11.0)	20.5±0.58 (19.5–21.6)
	♀	11	44.9±0.82 (43.7–46.0)	17.0±0.50 (15.9–17.7)	29.4±0.69 (28.2–30.8)	21.0±0.51 (20.0–21.7)	15.5±0.73 (14.4–16.9)	7.0±0.35 (6.4–7.6)	10.2±0.41 (9.6–11.0)	20.7±0.60 (19.3–21.6)
Biliran	♀	1	45.4	17.1	30.5	21.4	15.3	7.1	10.7	20.3

Note: Measurements other than weight are in millimeters.
* External measurements only.

ever, cranial measurements of males and females are comparable (table 17).

SPECIMENS EXAMINED—Total 61. LEYTE: Leyte PROV.: site L2 (14 USNM); site L15 (2 AMNH); site L8 (8 DMNH); site L9 (13 DMNH); site L10 (3 AMNH); site L11 (3 DMNH); site L12 (10 DMNH); site L13 (1 DMNH). BILIRAN: site B1 (2 USNM); site B3 (4 USNM); site B4 (1 UMMZ).

Family **Muridae**—Rats and Mice

Apomys littoralis (Sanborn, 1952)

The native mouse genus *Apomys* is one of the largest endemic Philippine murid genera, including eight currently recognized species (Heaney et al., 1987). Names previously used for *Apomys* species in the central Philippines were based on small numbers of poorly prepared specimens. In a review of the genus, Musser (1982a) referred to Leyte specimens as *A. microdon*. However, on the basis of preliminary examination of holotypes and the large series of specimens we collected, we use the name *littoralis* for animals from both Leyte and Biliran (as did Musser & Heaney, 1992). On Mt. Pangasugan, Leyte, *Apomys* were taken at all primary lowland, montane, and mossy forest sites between 320 and 950 m elevation (sites L3–L6) but were most common at the highest elevation (table 1; Heaney et al., 1989). They were also recorded at all primary lowland and montane forest sites on Biliran (sites B2–B4). None were taken on Maripipi despite considerable trapping effort (>900 trap-nights) in what appeared to be excellent habitat for them, and we consequently believe it unlikely that the species is present on Maripipi. Most of our specimens were trapped on the ground in areas with relatively dense cover, but some were taken where ground cover was sparse. Two pregnant females collected on 27 March and 2 April each contained two embryos (crown–rump lengths = 2–8 mm). Another female collected on 21 March had three placental scars. Most specimens collected between mid-March and late April were either non-breeding adults or immature animals. There is no apparent sexual or geographic size variation among specimens from Leyte and Biliran (table 18). Karyotypes of specimens from Leyte and Biliran are 2n = 44, FN = 88, representing the highest fundamental number recorded for Indo-Australian murines (Rickart & Musser, in press).

SPECIMENS EXAMINED—Total 78. LEYTE: Leyte PROV.: site L3 (2 USNM); site L4 (2 UMMZ, 7 USNM); site L5 (1 UMMZ, 6 USNM); site L6 (16 USNM); site L8 (4 DMNH); site L9 (8 DMNH); site L11 (6 DMNH); site L12 (9 DMNH); site L13 (1 DMNH). BILIRAN: site B2 (4 UMMZ); site B3 (4 USNM); site B4 (8 UMMZ).

Batomys salomonseni Sanborn, 1953

This native forest rat is restricted to the Mindanao faunal region (Musser & Heaney, 1992). On Mt. Pangasugan, Leyte, it was by far the most common species trapped in primary montane and mossy forest at 700 and 950 m elevation (sites L5 and L6), whereas it was rare or absent at sites in

TABLE 17. *Extended.*

Orbital length	Maxillary molariform toothrow	Palatal breadth at P4	Diastema length	Total length	Tail length	Hindfoot	Ear	Weight (g)
6.1	3.4 (3.3–3.4)	4.8 (4.7–4.9)	5.9 (5.8–6.2)	160 (159–160)	70 (69–71)	26 (25–27)	11 (11–12)	29.7
				172	75	25	12	32.0
14.9±0.52 (14.1–16.6)	8.4±0.28 (8.1–9.0)	10.4±0.28 (9.9–11.0)	11.5±0.37 (10.9–12.3)	354±15.8 (325–382)	164±9.7 (155–177)	48±1.6 (46–50)	21±0.64 (20–22)	233±19.1 (210–265)
14.8±0.34 (14.1–15.2)	8.5±0.24 (8.2–8.9)	10.4±0.32 (10.0–11.0)	11.3±0.39 (10.5–11.8)	337±17.0 (325–349)	156±7.8 (150–161)	48±0.7 (47–48)	20	207±2.8 (205–209)
14.2	8.3	10.1	11.1	363	165	49	19	235

lowland forest from 50 to 500 m elevation (table 1; Heaney et al., 1989). In contrast to the situation on Leyte, *Batomys* was rare on Biliran, where only three animals were trapped, all at sites above 700 m elevation (sites B2 and B3). It was not recorded on Maripipi despite considerable trapping effort in what appeared to be excellent habitat for the species. We believe it does not occur on that island. All of our specimens were taken in traps set on the ground, most in dense cover, in subsurface runways, or in root tangles at tree bases. Among the many specimens that we collected between mid-March and early April, none were in breeding condition. Included were several juveniles that were nearly full grown as well as adult females that were post-lactational. Single placental scars were noted in two females. Males in our sample average slightly larger than females in most cranial and external measurements (table 18). Leyte and Biliran specimens are comparable in size to specimens from Mindanao (Heaney & Rabor, 1982). Karyotypes of specimens from Leyte are 2n = 52, FN = 52, and consist entirely of telocentric chromosomes (Rickart & Musser, in press).

SPECIMENS EXAMINED—Total 40. LEYTE: Leyte PROV.: site L4 (1 USNM); site L5 (14 USNM); site L6 (21 USNM); site L8 (1 DMNH). BILIRAN: site B2 (2 UMMZ); site B3 (1 USNM).

Bullimus bagobus Mearns, 1905

This endemic rat is widespread in the Mindanao faunal region (Musser & Heaney, 1992). On Mt. Pangasugan, Leyte, we trapped this species in primary lowland forest at 300 and 500 m elevation (sites L3 and L4) but not in montane or mossy forest (table 1; Heaney et al., 1989). It was, however, taken in mossy forest at our highest elevation primary forest site on Maripipi (M4). The species was not recorded on Biliran despite moderate trapping effort in suitable low-elevation habitat. It may well be absent from Biliran, but more trapping, particularly in lower elevation forest, is required to confirm this. All specimens we trapped were taken on the ground, usually in relatively flat, open areas. A post-lactational female taken on 21 April had two placental scars. Males in our series are substantially larger than females (table 18). Cranial and external measurements of specimens from Leyte and Maripipi are similar to those for specimens from Dinagat and Siargao, whereas specimens from Mindanao have consistently larger cranial dimensions (table 18; Heaney & Rabor, 1982). A female from Leyte had a karyotype of 2n = 42, FN = 58, similar to many species of *Rattus* (Rickart & Musser, in press).

SPECIMENS EXAMINED—Total 29. LEYTE: Leyte PROV.: site L3 (6 USNM); site L4 (1 UMMZ, 2 USNM); site L9 (13 DMNH). MARIPIPI: site M4 (7 USNM).

Crunomys rabori Musser, 1982

This species is known only from the holotype collected near Buri (site L8) in northern Leyte (Musser, 1982b). Failure to obtain additional specimens during our survey of Mt. Pangasugan suggests that the species may be rare. However,

TABLE 18. Means (± SD) and ranges of selected measurements of adult murid rodents (*Apomys, Batomys, Bullimus,* and *Crunomys*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Basioccipital length	Interorbital width	Zygomatic breadth	Mastoid breadth	Nasal length	Anterior nasal breadth	Rostral depth	Rostral length
Apomys cf. *littoralis*										
Leyte	♂	22	25.8±0.60 (24.9–26.9)	5.0±0.19 (4.7–5.3)	13.9±0.37 (13.3–14.5)	12.0±0.31 (11.4–12.8)	10.5±0.51 (9.7–11.6)	3.5±0.28 (3.1–4.1)	6.0±0.21 (5.5–6.4)	10.9±0.48 (10.2–12.0)
	♀	16	25.9±0.63 (24.9–27.0)	5.0±0.19 (4.7–5.2)	13.9±0.47 (13.1–14.5)	11.7±0.47 (10.3–12.4)	10.8±0.40 (10.2–11.5)	3.5±0.21 (3.2–3.9)	6.0±0.23 (5.6–6.4)	11.0±0.28 (10.4–11.5)
Biliran	♂	6	25.9±0.67 (25.2–26.9)	4.9±0.15 (4.7–5.1)	13.3±0.23 (13.0–13.5)	11.7±0.14 (11.5–11.8)	10.6±0.40 (10.2–11.2)	3.6±0.21 (3.3–3.9)	5.9±0.14 (5.7–6.1)	11.0±0.37 (10.5–11.4)
	♀	5	26.1±0.55 (25.6–27.0)	4.9±0.14 (4.7–5.0)	13.7±0.26 (13.5–14.1)	11.6±0.22 (11.3–11.9)	10.5±0.40 (10.2–11.1)	3.6±0.18 (3.4–3.9)	6.0±0.21 (5.8–6.3)	11.1±0.40 (10.6–11.5)
Batomys salomonseni										
Leyte	♂	8	39.5±1.06 (38.1–40.8)	6.2±0.29 (5.8–6.6)	21.9±0.57 (21.3–23.1)	15.9±0.41 (15.6–16.7)	17.6±0.91 (16.0–18.8)	5.3±0.27 (5.0–5.8)	9.5±0.43 (9.0–10.3)	18.3±0.66 (17.5–19.1)
	♀	6	38.3±1.14 (37.0–39.5)	6.2±0.19 (5.9–6.4)	21.2±0.79 (19.9–21.9)	15.4±0.56 (14.7–16.0)	17.4±0.70 (16.0–17.8)	5.2±0.28 (4.8–5.5)	9.0±0.34 (8.6–9.6)	18.1±0.65 (16.8–18.5)
Biliran	♂	1	36.1	6.0	21.7	—	19.1	5.7	10.4	18.8
	♀	1		6.1	20.9	14.9	16.0	5.0	9.0	16.4
Bullimus bagobus										
Leyte	♂	9	57.1±1.52 (55.1–58.5)	8.1±0.39 (7.6–8.8)	29.5±1.53 (27.6–31.2)	18.2±0.87 (17.3–19.6)	24.6±1.31 (23.0–26.8)	6.5±0.43 (5.9–7.2)	13.0±0.67 (12.2–13.7)	26.2±1.10 (24.6–27.7)
	♀	7	56.5±2.59 (54.7–59.5)	8.0±0.38 (7.4–8.5)	28.6±0.54 (27.9–29.4)	18.1±0.79 (17.3–18.9)	24.0±0.71 (23.1–25.2)	6.3±0.30 (5.9–6.8)	12.6±0.66 (11.9–13.8)	25.9±0.82 (24.7–27.1)
Maripipi	♂	1	57.0	8.7	29.7	18.7	26.1	5.8	13.8	24.7
	♀	1	53.6	8.1	28.1	—	24.2	5.6	12.4	24.8
Crunomys rabori										
Leyte	♂	1	30.6	6.1	—	12.1	12.9	3.7	6.7	—

Note: Measurements other than weight are in millimeters.

our standard trapping techniques (live and snap traps baited with coconut and peanut butter) may simply have been ineffective with this species, as they have proved to be with some other Philippine murids (Rickart et al., 1991). Two other species of *Crunomys, C. fallax* from Luzon and *C. melanius* from Mindanao, are also very poorly known. Musser and Heaney (1992) suggested that morphological differences between *rabori* and *melanius* might represent age variation and recommended further investigation. Selected cranial measurements of *C. rabori* appear in Table 18.

SPECIMENS EXAMINED—Total 1. LEYTE: Leyte Prov.: site L8 (1 DMNH).

Mus musculus castaneus Waterhouse, 1843

The cosmopolitan commensal house mouse occurs throughout the Philippines in and around human dwellings. We obtained none on Leyte, but there are previous records from that island. We trapped two specimens in buildings on Maripipi. Although there are no records from Biliran, house mice almost certainly occur there.

SPECIMENS EXAMINED—Total 8. LEYTE: Leyte Prov.: site L9 (2 DMNH); site L13 (4 DMNH). MARIPIPI: site M5 (1 USNM); site M6 (1 USNM).

Rattus everetti (Gunther, 1879)

This widespread native species of *Rattus* occurs throughout the Luzon, Mindanao, and Mindoro faunal regions, from sea level to 2400 m elevation (Musser & Heaney, 1992). On Mt. Pangasugan, Leyte, this species was present at all primary forest sites (sites L3–L6) but was most common in lowland forest (table 1; Heaney et al., 1989). It was also recorded in disturbed forest at 50 m elevation (site L2). On Biliran, *Rattus everetti* was the most

TABLE 18. *Extended.*

Orbital length	Maxillary molariform toothrow	Palatal breadth at P4	Diastema length	Total length	Tail length	Hindfoot	Ear	Weight (g)
9.3±0.38 (8.8–10.0)	5.4±0.14 (5.0–5.6)	5.9±0.22 (5.4–6.3)	6.7±0.26 (6.3–7.3)	235±6.6 (225–248)	134±6.5 (127–148)	30±0.9 (28–32)	18±1.1 (17–20)	30.3±2.55 (27.0–34.5)
9.3±0.29 (8.8–9.8)	5.4±0.14 (5.2–5.7)	6.0±0.21 (5.7–6.5)	6.8±0.30 (6.3–7.4)	237±9.5 (224–250)	138±6.1 (136–149)	30±1.0 (28–31)	18±1.5 (16–20)	32.5±3.14 (28.4–39.4)
9.3±0.17 (9.1–9.5)	5.4±0.15 (5.3–5.7)	5.9±0.14 (5.7–6.1)	6.5±0.12 (6.4–6.7)	239±6.9 (231–247)	140±5.5 (132–146)	32±0.8 (31–33)	18±1.3 (16–19)	30±4.0 (24–35)
9.5±0.25 (9.1–9.7)	5.2±0.15 (5.1–5.4)	5.8±0.19 (5.5–6.0)	6.9±0.33 (6.6–7.4)	239±8.1 (230–246)	137±5.0 (132–142)	30±1.7 (29–32)	19±0.5 (19–20)	31±3.2 (27–36)
13.5±0.38 (13.0–14.1)	8.0±0.28 (7.5–8.4)	7.4±0.26 (7.0–7.8)	11.1±0.35 (10.6–11.6)	333±18.1 (313–358)	152±9.8 (140–167)	39±1.1 (38–41)	23±0.8 (22–24)	205±33.4 (165–255)
12.9±0.41 (12.5–13.5)	7.9±0.21 (7.6–8.2)	7.4±0.19 (7.2–7.7)	10.6±0.41 (10.2–11.2)	328±16.2 (306–347)	151±7.0 (140–158)	39±1.2 (38–41)	22±1.0 (21–24)	178±26.4 (147–215)
14.2	8.0	7.2	12.2	337	148	37	22	220
12.9	7.8	7.0	10.5	308	142	37	22	145
20.6±0.73 (19.9–21.9)	9.9±0.35 (9.4–10.4)	10.3±0.54 (9.7–11.4)	17.1±1.14 (15.8–19.2)	460	195	52	26	445
20.2±0.91 (19.2–21.4)	9.6±0.19 (9.4–9.8)	9.7±0.49 (9.3–10.6)	16.8±1.05 (16.1–19.1)	434±1.0 (430–438)	191±7.1 (186–196)	52±0.7 (52–53)	28±2.1 (26–29)	425±21.1 (410–440)
20.4	9.7	10.1	17.3	457	194	58	30	520
19.5	9.8	10.0	15.5	403	175	54	29	340
–	3.9	5.8	8.7	–	–	–	–	–

common species trapped in primary montane forest (site B3). It was also common in partially logged primary forest at 700 m (site B2) and was present in ridgetop mossy forest at 950 m (site B4). This species was relatively common in primary mossy forest between 600 and 800 m elevation on Maripipi (site M4). Our specimens were trapped in a wide variety of microhabitats. Most were trapped on the ground in areas with moderate to dense cover, but many were taken in traps set on inclined tree trunks or other elevated situations up to 2 m above the forest floor. None of the specimens collected by us during the months of March and April were in breeding condition. Three females taken between 19 and 29 March contained four, five, and six old placental scars. Data from elsewhere in the Philippines indicate that *Rattus everetti* does not breed between late February and early May (Heaney et al., 1991; Rickart et al., 1991). Although there is no apparent sexual or geographic size variation among our samples (table 19), cranial and external measurements are consistently smaller than those for specimens from Dinagat, Siargao, and Mindanao (Heaney & Rabor, 1982). Specimens from Leyte, Biliran, Catanduanes, and Luzon share a karyotype of 2n = 42, FN = 62, which is similar to those documented for many other species of *Rattus* (Rickart & Musser, in press).

SPECIMENS EXAMINED—Total 57. LEYTE: Leyte PROV.: site L2 (1 USNM); site L3 (9 USNM); site L4 (1 UMMZ, 11 USNM); site L5 (1 UMMZ, 8 USNM); site L6 (4 USNM). BILIRAN: site B2 (4 UMMZ); site B3 (11 USNM); site B4 (1 UMMZ). MARIPIPI: site M4 (6 USNM).

Rattus exulans (Peale, 1848)

This non-native commensal rat species occurs from Bangladesh to Easter Island and is found throughout the Philippines. It is often abundant in agricultural situations but is usually rare in forest (Heaney et al., 1989, 1991). On Biliran, we

TABLE 19. Means (± SD) and ranges of selected measurements of adult murid rodents (*Rattus*) from Leyte, Biliran, and Maripipi islands.

	Sex	N	Basioc-cipital length	Inter-orbital width	Zygomatic breadth	Mastoid breadth	Nasal length	Anterior nasal breadth	Rostral depth	Rostral length
Rattus everetti										
Leyte	♂	5	48.3±0.65 (47.6–49.0)	7.5±0.47 (7.0–8.0)	24.8±0.63 (23.9–25.5)	19.9±0.41 (19.5–20.4)	19.6±0.65 (19.3–20.8)	5.7±0.40 (5.2–6.2)	11.5±0.33 (11.0–11.9)	19.0±0.82 (18.1–20.1)
	♀	8	48.7±1.65 (48.3–50.6)	7.3±0.14 (7.1–7.5)	25.1±0.89 (23.7–26.5)	19.5±0.54 (18.7–20.3)	19.6±1.11 (18.1–21.2)	5.6±0.19 (5.2–5.8)	11.3±0.32 (10.9–11.8)	19.3±0.96 (18.2–21.2)
Biliran	♂	6	48.8±2.49 (45.6–51.1)	7.3±0.50 (6.8–7.4)	25.3±1.18 (24.0–27.1)	19.8±0.49 (19.3–20.5)	19.7±1.00 (18.6–20.9)	5.5±0.41 (5.0–6.1)	11.1±0.76 (10.0–12.2)	19.5±1.09 (18.1–20.6)
	♀	3	47.7 (46.1–48.5)	7.4 (6.7–7.8)	25.3 (24.8–25.7)	19.3 (19.0–19.4)	19.8 (18.8–20.6)	5.5 (5.3–5.7)	11.0 (10.8–11.1)	19.0 (17.9–19.8)
Maripipi	♀	2	48.2 (46.2–50.2)	7.4 (7.2–7.6)	24.7 (24.0–25.4)	19.3 (18.8–19.8)	19.8 (18.8–20.9)	5.1 (4.6–5.6)	11.4 (11.0–11.9)	19.1 (18.0–20.2)
Rattus exulans										
Leyte	♂	5	29.8±0.70 (29.0–30.7)	5.0±0.19 (4.8–5.3)	15.4±0.36 (15.1–15.9)	12.7±0.92 (11.1–13.4)	12.0±0.98 (10.8–12.2)	3.4±0.17 (3.3–3.7)	6.6±0.19 (6.4–6.9)	11.3±0.40 (10.8–11.8)
	♀	1	29.7	4.9	15.4	12.9	11.0	3.3	6.3	11.2
Rattus rattus										
Leyte	♂	9	44.4±1.59 (42.0–47.5)	6.6±0.35 (5.9–7.1)	21.8±0.89 (20.7–23.8)	16.9±0.43 (16.5–18.0)	16.6±1.20 (14.9–18.6)	4.9±0.24 (4.5–5.2)	9.9±0.31 (9.5–10.5)	16.6±0.96 (15.2–18.6)
	♀	3	45.2 (44.5–45.6)	6.6 (6.4–6.9)	22.4 (21.6–23.2)	17.6 (16.8–18.6)	16.8 (16.5–17.1)	5.1 (4.5–5.5)	10.0 (9.8–10.4)	16.8 (16.6–16.9)
Biliran	♂	7	41.8±1.82 (39.3–44.0)	6.7±0.35 (6.2–7.3)	21.3±0.70 (20.0–22.2)	17.1±0.89 (15.7–18.4)	16.1±1.00 (14.6–17.1)	5.1±0.62 (4.1–5.7)	9.7±0.59 (8.7–10.5)	16.2±0.78 (15.0–16.9)
	♀	3	39.2 (39.0–39.3)	6.5 (6.3–6.8)	21.0 (20.2–22.0)	16.2 (16.2–16.3)	15.2 (14.3–15.9)	4.9 (4.8–5.0)	9.1 (8.8–9.8)	15.3 (14.2–16.2)
Maripipi	♂	2	42.6 (40.5–44.8)	6.6 (5.9–7.3)	21.1 (20.0–22.2)	17.1 (16.2–18.0)	16.4 (15.9–16.9)	4.8 (4.3–5.2)	9.4 (8.5–10.3)	16.6 (15.4–17.8)
	♀	3	39.5 (37.0–42.0)	6.2 (6.0–6.3)	20.9 (19.1–22.0)	16.4 (16.1–16.6)	14.8 (13.3–16.6)	4.6 (4.3–4.8)	8.8 (8.2–9.5)	15.0 (13.9–16.2)

Note: Measurements other than weight are in millimeters.

trapped two specimens on the ground in disturbed forest at 700 m elevation (site B2). Although there are previous records for this species on Leyte, we did not encounter it on that island or on Maripipi. However, we did limited trapping in areas where commensal species were likely to occur. Measurements appear in Table 19.

SPECIMENS EXAMINED—Total 8. LEYTE: Leyte Prov.: site L13 (6 DMNH). BILIRAN: site B2 (2 UMMZ).

Rattus rattus mindanensis (Mearns, 1905)

This non-native commensal species is widespread in Asia and is found throughout the Philippines (Musser, 1977; Heaney et al., 1987). It is most often found in urban and agricultural areas but is sometimes encountered in forest, particularly in areas that have been disturbed. On Leyte, we collected specimens in buildings on the campus of the Visayas State College of Agriculture and trapped a single specimen in an area of second growth at 50 m elevation (site L2; Heaney et al., 1989). This species was recorded at all of our trapping sites on Biliran. It was the only species trapped in forest plantation and agricultural land at 450 m (site B1) and was the most common species in disturbed forest at 700 m (site B3; table 1). On Maripipi, the species was taken in agricultural land, disturbed forest, and undisturbed primary forest as high as 800 m elevation. Three females taken between 18 and 26 April contained four, six, and seven embryos. Cranial and external measurements appear in table 19. Specimens from Biliran and Negros have a karyotype of 2n = 42, FN = 60, resembling those documented for specimens from elsewhere in Asia (Rickart & Musser, in press).

TABLE 19. *Extended.*

Orbital length	Maxillary molariform toothrow	Palatal breadth at P4	Diastema length	Total length	Tail length	Hindfoot	Ear	Weight (g)
17.8±0.47	9.0±0.19	9.1±0.34	13.6±0.39	464±18.6	239±12.6	46±1.3	26±1.1	260±10.4
(17.4–18.4)	(8.7–9.1)	(8.8–9.6)	(13.2–14.1)	(440–484)	(224–256)	(45–48)	(25–27)	(248–270)
18.4±0.52	8.9±0.26	8.9±0.33	13.8±0.83	473±13.9	246±7.4	46±1.2	26±0.5	249±26.7
(17.5–19.1)	(8.4–9.2)	(8.2–9.3)	(12.5–14.9)	(455–495)	(233–253)	(43–47)	(26–27)	(197–280)
17.9±0.86	9.0±0.26	9.2±0.35	13.6±1.19	472±26.1	242±12.4	47±1.0	25±1.4	278±43.2
(17.1–18.9)	(8.7–9.4)	(8.7–9.6)	(12.2–15.1)	(434–506)	(222–256)	(46–48)	(25–28)	(235–255)
17.8	8.9	8.9	13.0	448	231	44	25	242
(17.1–18.2)	(8.9–9.0)	(8.8–8.9)	(12.4–13.5)	(432–457)	(220–245)	(43–45)	(24–25)	(235–250)
18.0	8.8	8.9	13.5	465	237	48	26	248
(17.7–18.4)	(8.8–8.9)	(8.8–9.0)	(12.6–14.4)	(437–493)	(228–245)	(47–50)	(25–27)	(215–280)
11.2±0.34	5.4±0.18	6.2±0.21	8.0±0.22	–	–	–	–	–
(10.7–11.6)	(5.2–5.7)	(5.9–6.4)	(7.8–8.3)					
11.5	5.4	6.1	8.2	–	–	–	–	–
16.3±0.74	7.5±0.09	8.4±0.23	12.5±0.66	–	–	–	–	–
(15.3–17.3)	(7.4–7.7)	(8.1–8.9)	(11.4–13.8)					
16.7	7.6	8.9	12.9	–	–	–	–	–
(16.5–16.8)	(7.3–7.8)	(8.6–9.1)	(12.2–13.5)					
15.2±0.71	7.6±0.31	8.2±0.31	11.8±0.80	404±13.4	204±5.4	38±2.5	24±0.5	209±19.3
(13.9–16.2)	(7.4–8.2)	(7.8–8.8)	(0.9–13.3)	(385–422)	(197–210)	(36–41)	(23–24)	(200–235)
14.6	7.3	8.5	11.3	372	195	36	23	145
(14.0–15.4)	(7.0–7.5)	(8.2–8.8)	(10.9–12.1)	(372–373)	(192–200)	(35–37)	(23–24)	(140–150)
16.1	7.4	8.3	11.8	394	196	36	24	198
(15.8–16.4)		(7.9–8.7)	(10.8–12.8)	(373–416)	(191–201)	(36–37)	(23–24)	(155–240)
14.6	7.4	8.0	10.8	362	189	39	24	155
(13.7–15.4)	(7.1–7.7)	(7.7–8.2)	(9.6–11.9)	(325–392)	(171–206)	(37–41)		(107–182)

SPECIMENS EXAMINED—Total 54. LEYTE: Leyte Prov.: site L1 (2 USNM); site L2 (1 USNM); site L15 (4 AMNH); site L9 (10 DMNH); site L10 (7 AMNH); site L13 (1 DMNH); site L16 (4 FMNH). BILIRAN: site B1 (4 USNM); site B2 (3 UMMZ); site B3 (5 USNM); site B4 (3 UMMZ). MARIPIPI: site M1 (4 UMMZ); site M4 (5 USNM); site M10 (1 UMMZ).

Order **Carnivora**
Family **Viverridae**—Civets

Paradoxurus hermaphroditus philippinensis Jourdan, 1837

The palm civet occurs from India to Southeast Asia and is widespread in the Philippines. On Leyte, we trapped one animal in primary lowland forest at 320 m elevation (site L3) and shot a second individual from a tree in an area of mixed agriculture and second growth at 50 m elevation (site L2). We received reports of civets on both Biliran and Maripipi but obtained no specimens. The descriptions given by most informants conformed to that of the palm civet. On both islands we also found civet scats that most closely resembled those of *Paradoxurus* (i.e., composed primarily of seeds; Heideman et al., 1987).

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L2 (1 USNM); site L3 (1 USNM).

Viverra tangalunga Gray, 1832

The Malay civet (or tangalung) is found from peninsular Malaysia to Sulawesi. Although it is

widespread in the Philippines, its presence on Leyte was not documented until our field work in 1987. The species is probably present in all forested habitats on Leyte. On Mt. Pangasugan, we trapped an immature male in primary lowland forest at 320 m elevation (site L3) and a lactating adult female in ridgetop mossy forest at 1000 m (site L6). The tangalung is more carnivorous than is *Paradoxurus* (Heideman et al., 1987). Stomach contents of the adult female included two large centipedes (ca. 15–20 cm long), one large snail, and remains of at least one skink and one small snake. This species has not been documented from Maripipi or Biliran.

SPECIMENS EXAMINED—Total 2. LEYTE: Leyte Prov.: site L3 (1 USNM); site L6 (1 USNM).

Order **Artiodactyla**
Family **Suidae**—Pigs

Sus barbatus mindanensis Major, 1897

The bearded pig occurs on the Malay Peninsula, Borneo, and throughout the Philippines. On Leyte, we purchased nine specimens (old trophy skulls or mandibles) that local hunters had taken from the vicinity of Mt. Pangasugan. During our field work on the mountain, we saw old pig wallows at 300 and 950 m elevation. In 1987 local farmers reported that pigs were moderately common on Mt. Pangasugan but had declined from previous years. In 1984 we purchased a pig mandible on Biliran from a pig that had been killed by a local hunter several years previously. In 1987 we saw pig trails and wallows in primary forest between 700 and 950 m elevation and encountered a group of pig hunters near site B3. In contrast, local hunters on Maripipi had never seen or heard of wild pigs there. Although principally denizens of forest, wild pigs are encountered in agricultural land, where they reportedly raid a variety of crops (usually at night). They are heavily hunted both as a source of meat and in response to crop depredations. Hunters generally track pigs with dogs or trap them along game trails with snares, deadfalls, or concealed pit traps. They reportedly travel in groups, often sows accompanied by several piglets.

SPECIMENS EXAMINED—Total 10. LEYTE: Leyte Prov.: vicinity of Mt. Pangasugan (9 USNM). BILIRAN: unknown locality (1 UMMZ).

Family **Cervidae**—Deer

Cervus mariannus Desmarest, 1822

This species occurs in the Mariana Islands and the Philippines. It is found on most of the larger Philippine islands except Cebu, Masbate, Negros, and Panay. Hunting and forest destruction have seriously reduced populations and caused local extinction in many areas (Heaney et al., 1987). On Leyte, we obtained several deer skulls from local hunters in the Mt. Pangasugan region. According to local farmers, deer formerly were common on the mountain but were quite rare by 1987 due to overhunting. At that time none had been taken in well over a year. We obtained no deer specimens on Biliran. In 1987 local hunters on Biliran claimed that deer had been present in the recent past but were now possibly extinct. In contrast, inhabitants of Maripipi informed us that they had never seen or heard of any deer on their island.

Cervus mariannus and *C. alfredi* were formerly included within *C. unicolor* but were recognized as distinct species by Grubb and Groves (1983). *Cervus alfredi* is currently found only on Negros and Panay. The species formerly occurred on Cebu, Guimaras, and Masbate, where it is now extinct (Cox, 1987). Cox (1987) also reported *C. alfredi* from Leyte on the basis of unverified reports, but we are unaware of any specimens and consider this record questionable. The two species of Philippine deer are readily distinguishable by adult coloration; *C. alfredi* has a distinctive pattern of pale dorsal spots on a brown coat, whereas *C. mariannus* lacks spots. Reliable informants in the Mt. Pangasugan region reported that all local deer lacked spots (except when fawns), thus identifying them as *C. mariannus*.

SPECIMENS EXAMINED—Total 5. LEYTE: Leyte Prov.: vicinity of Mt. Pangasugan (1 USNM); site L18 (1 VISCA); site L22 (3 VISCA).

Analysis and Discussion

Adequacy of Sampling Effort

Before analyzing the results of our surveys, we must consider how closely current data reflect actual species richness on these islands. Our experience has shown that the widest possible range of habitats must be investigated to ensure adequate

sampling of faunas in the Philippines (Heaney et al., 1989, 1991; Rickart et al., 1991). On all islands, we visited forested sites along broad elevational gradients encompassing lowland, montane, and mossy forest habitats. However, we were constrained by the current extent of remaining forested habitats. On Biliran in particular, extensive illegal logging had severely reduced lowland and mid-elevation forest at the time of our surveys. We were also constrained by island area: the extent of mossy forest on Maripipi (ca. 1 km^2) is limited by the small area of high elevation. On each island we also sampled along disturbance gradients ranging from primary forest to secondary forest, second growth, and mosaics of second growth and agricultural land. However, our sampling efforts in the most disturbed habitats were limited, particularly with respect to trapping. Finally, we investigated local caves that were reported to us on each island and collected bats when they were present.

The adequacy of sampling may be assessed with species–effort curves that plot the cumulative number of species recorded against sampling time (Rickart et al., 1991). We used this method to examine the relative success of our netting and trapping surveys for different groups on the three islands. To be a true measure of sampling effectiveness, this approach requires that sampling be conducted over the full range of available habitats using methods that ensure capturing the largest number of species (i.e., careful placement of nets and traps to cover a variety of sites and standardization of netting and trapping procedures). We believe that our surveys meet this requirement.

On Leyte, our small mammal trapping at four primary forest sites on Mt. Pangasugan (sites L3–L6) yielded a total of five species of insectivores and murid rodents (table 1). A species–effort curve shows that the total number of species was reached well before the midpoint of our survey (fig. 16A). Had our initial efforts been evenly distributed in both lowland and highland habitats, the total would certainly have been reached earlier. The distinct asymptote of this curve suggests that the occurrence of additional species along this particular transect is unlikely. Similarly, curves generated from our netting results for both small fruit bats and microchiropteran bats on Mt. Pangasugan also are asymptotic (fig. 16B). However, given the gradual accrual rate for microchiropterans, we predict that substantial sampling would yield some additional species in this group.

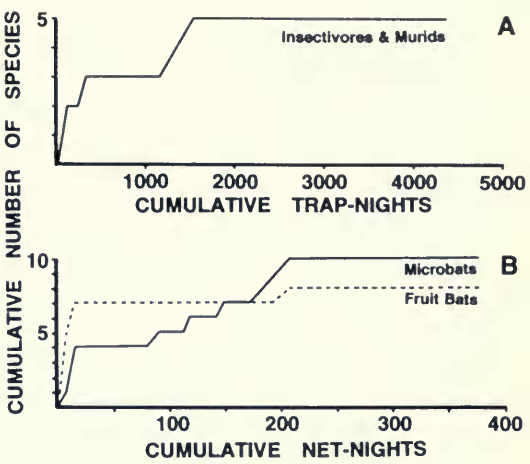

FIG. 16. Species–effort curves for surveys of (A) insectivores and murid rodents and (B) small fruit bats and microchiropteran bats on Mt. Pangasugan, Leyte.

Our survey efforts were more extensive on Leyte than on either of the smaller islands (tables 1, 5, 10). Whereas work on Leyte was specifically conducted to ascertain patterns of variation over habitat gradients, the Biliran and Maripipi surveys were conducted primarily to determine island species richness. However, our early efforts on the smaller islands were undoubtedly more effective because they were initiated over a broader range of habitats. For non-volant small mammals (insectivores and murid rodents), the cumulative number of species appeared to reach an asymptote before the end of the sampling effort on both Biliran and Maripipi (fig. 17A), although the presence of additional species on both islands cannot be discounted from these curves. For small fruit bats (i.e., excluding *Acerodon* and *Pteropus*), the cumulative number of species quickly reached an asymptote on Maripipi (fig. 17B). On Biliran, where our netting efforts were almost entirely confined to forested habitats, the number of fruit bat species reached an early plateau that was maintained until the very end of our survey, when we sought and quickly found the widespread species *Rousettus amplexicaudatus* in lowland agricultural land (fig. 17B). On both islands, the number of microchiropterans slowly increased with time, showing no indication of reaching asymptotes (fig. 17C). We expect more microchiropteran species to be found on both islands.

We conclude from these curves that our surveys were extensive although not necessarily exhaus-

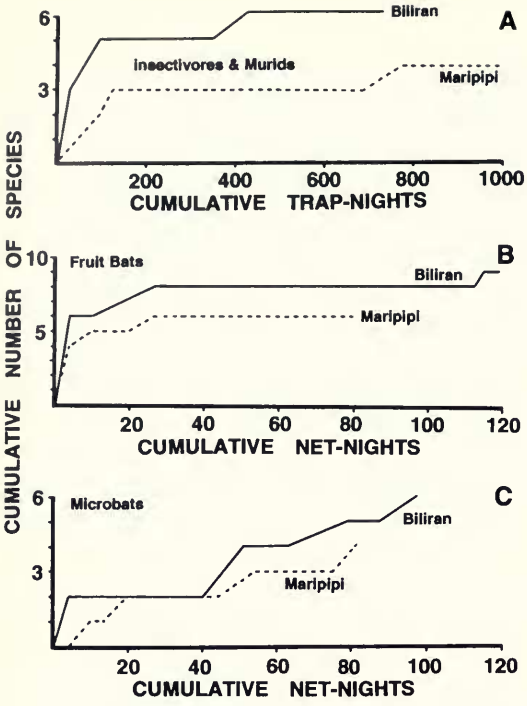

FIG. 17. Species–effort curves for surveys of (A) insectivores and murid rodents, (B) small fruit bats, and (C) microchiropteran bats on Biliran and Maripipi.

tive. On Leyte, where our field efforts were most thorough and records from earlier collectors are available, we believe that data are fairly accurate in reflecting true species richness. Data for the smaller islands, derived solely from our own survey efforts, must be viewed as less complete, specifically for microchiropteran bats.

Because species differed in how easily they were observed or captured, the accuracy of our sampling efforts varied as a function of both taxonomic group and survey method. To account for this in our analyses, we consider patterns among five separate groups of species that are categorized by both taxonomy and sampling methodology: (1) insectivorous bats that generally are difficult to capture with mist nets or must be collected at roost sites, (2) large pteropodid bats (genera *Acerodon* and *Pteropus*) that are seldom captured in mist nets and generally must be collected at roost sites, (3) small pteropodid bats (all other genera) that are readily captured in mist nets, (4) non-volant species that are readily captured in small mammal traps (insectivores and murid rodents), and (5) non-volant species that are large or otherwise difficult to trap but are readily documented through sightings, sign, or local reports (dermopterans, primates, sciurid rodents, carnivores, and ungulates).

Biogeography

The islands of Leyte, Biliran, and Maripipi currently are known to support respectively 45, 30, and 25 indigenous species of land mammals. Collectively, a total of 48 native and 4 introduced commensal species are known from the three islands (table 20).

INSECTIVOROUS BATS—Twenty species of insectivorous bats representing six families have been recorded from the three islands: 17 on Leyte and 8 each on Biliran and Maripipi (table 20). Because most microchiropterans are relatively difficult to sample, our understanding of this group is less complete than for other groups, and we expect more species to be found on all three islands. In part, the more than 2-fold difference in the number of species on Leyte compared to the smaller islands undoubtedly reflects differences in total sampling effort (three to four times as many net-nights plus records from previous collectors). However, a reduction in the number of species with island area may also be a factor, as is the case for both fruit bats and non-volant mammals (Heaney, 1986, 1991a).

An important difference between island microchiropteran faunas that clearly is independent of sampling variation involves the distribution of the most common species. *Rhinolophus inops* was by far the most frequently netted species on both Leyte and Biliran, representing 50.6% and 82.6% of the total microchiropterans captured on the respective islands. This species was not recorded on Maripipi, and the most frequently netted species there, *Hipposideros obscurus,* was not recorded on either of the other islands (table 20).

All but one of the microchiropteran species recorded from the three islands have been recorded on *Mindanao.* The exception, *Harpiocephalus harpia,* is a widespread but rarely collected species that probably does occur there (Ingle & Heaney, 1992). Mindanao is known to support an additional 18 species of microchiropterans (Heaney et al., 1987).

LARGE FRUIT BATS—Large pteropodid bats commonly fly above and forage at the top of the forest canopy and therefore are difficult to sample with nets (Heideman & Heaney, 1989). Accordingly, our knowledge about the distribution of this group is incomplete. Four species are known from Leyte, three of which have been recorded on Maripipi. None have been collected on Biliran, but we sighted at least one species (probably *Acerodon jubatus*; table 20). All four, plus one additional species, occur on Mindanao (Heaney, 1991a).

SMALL FRUIT BATS—This is one of the groups for which we have high sampling confidence. We recorded a total of nine species, all of which occur on both Leyte and Biliran (table 20). *Haplonycteris fischeri* and *Ptenochirus minor,* among the most common species found at forested sites on both Leyte and Biliran, were not taken on Maripipi and probably do not occur there. Mindanao supports all nine species in this category plus three additional species of small fruit bats (Heaney, 1991a).

INSECTIVORES AND MURID RODENTS—A total of 10 species are included in this category: two insectivores and eight murid rodents (table 20). All have been recorded on Leyte, six on Biliran, and five on Maripipi. If introduced commensals are discounted, there are six native species on Leyte (one insectivore and five murids). One of these, *Crunomys rabori,* is a rarely caught Leyte endemic. We have fairly high sampling confidence for the remaining five indigenous species. Two of these, *Crocidura beatus* and *Rattus everetti,* were recorded on all three islands. *Bullimus bagobus,* a species that was relatively common in low-elevation forest on Leyte and in high-elevation forest on Maripipi, was not taken on Biliran and may not occur there. *Apomys littoralis* and *Batomys salomonseni* were among the most common small mammal species at forested sites on Leyte, particularly at high elevations (table 20). Both species were recorded at forest sites on Biliran, but neither were taken in similar habitat on Maripipi, where we doubt they occur.

Except for *Crunomys rabori,* all of the native species in this category occur on Mindanao. The sister-species of *Crunomys rabori* (*C. melanius*) does occur on Mindanao, together with eight additional endemic species of insectivores and murid rodents (Heaney, 1986; Musser & Heaney, 1992).

PRIMATES, SQUIRRELS, AND LARGE MAMMALS—A total of nine species fall into this category: one dermopteran, two primates, two squirrels, two carnivores, and two ungulates (table 20). Except for the carnivores, our sampling confidence for these species is high. All species in this group occur on Leyte, and all but one (*Viverra tangalunga*) are either known or reported from Biliran. In contrast, only the primates, dermopteran, and one carnivore species are known from Maripipi. We are fairly certain that four species in this category (the squirrels and ungulates) do not occur on Maripipi.

Eight of the nine species included in this category occur on Mindanao. The ninth, *Sundasciurus samarensis,* is very closely related to, and may be a subspecies of, *S. philippinensis,* which occurs on Mindanao (Heaney, 1979; Heaney et al., 1987). The Mindanao fauna includes an additional squirrel species, *Petinomys crinitus* (Heaney, 1986).

OVERVIEW—The terrestrial mammal faunas of Leyte, Biliran, and Maripipi are definitely derived from the richer fauna of the large southern island of Mindanao. Mindanao is known to support all but 3 of the 48 native species recorded from the three smaller islands. The exceptions include a widespread but rarely collected insectivorous bat that probably occurs on Mindanao and two rodents whose sister-species occur there. Of the remaining 45 species, 9 are restricted to the Mindanao faunal region, 10 are more widely distributed in the oceanic Philippines, and 25 have distributions that extend outside of the Philippines (table 20).

The faunal similarities of these islands reflect the fact that all were once incorporated within the late Pleistocene island of Greater Mindanao (Heaney, 1986, 1991a). Although Greater Mindanao may have supported some species with locally isolated distributions, it is reasonable to assume that a common fauna occurred throughout most of that land mass, as is true today on Mindanao (Musser & Heaney, 1992). Accordingly, our working hypothesis is that most faunal differences between the present-day islands stem from events that have occurred during the last 12,000 years (i.e., since the breakup of Greater Mindanao).

Evidence indicates that selective extinction has played the predominant (if not sole) role in shaping the faunas of these islands since the late Pleistocene. The process clearly has been influenced by island size: for both fruit bats and non-volant native mammals, species richness is highly correlated with island area (Heaney, 1986, 1991a). The island faunas also constitute a nested series (*sensu* Patterson & Atmar, 1986) ordered by island size. There are 24 species belonging to groups for which we have relatively high sampling confidence (i.e., all taxa except microchiropterans, flying foxes, and commensal species). Of these, only one (*Bullimus bagobus*) deviates from perfect nesting (table 20). Furthermore, if we consider the sister-species relationships within the genera *Sundasciurus* and *Crunomys,* the Leyte fauna is, in turn, perfectly nested within that of Mindanao.

Susceptibility to extinction is one factor that may result in the nested subset pattern (Patterson & Atmar, 1986). Examination of species that are present on Leyte and Biliran but absent on Maripipi does suggest that extinctions have been selective rather than random. Large species such as *Cervus mariannus* and *Sus barbatus* are probably particularly vulnerable on small islands because they

TABLE 20. List of land mammals recorded from Leyte, Biliran, and Maripipi islands.

	Distribution*	Leyte	Biliran	Maripipi	Totals
Insectivora					
Crocidura beatus	MIND	x	x	x	
Suncus murinus†	WIDE	x			
Dermoptera					
Cynocephalus volans	MIND	x	x	sighted	
Chiroptera					
Acerodon jubatus	PHIL	x	sighted?	x	
Cynopterus brachyotis	WIDE	x	x	x	
Eonycteris robusta	PHIL	x	x	x	
Eonycteris spelaea	WIDE	x	x	x	
Haplonycteris fischeri	PHIL	x	x		
Harpyionycteris whiteheadi	PHIL	x	x	x	
Macroglossus minimus	WIDE	x	x	x	
Ptenochirus jagori	PHIL	x	x	x	
Ptenochirus minor	MIND	x	x		
Pteropus hypomelanus	WIDE	x		x	
Pteropus pumilus	PHIL	x		x	
Pteropus vampyrus	WIDE	x			
Rousettus amplexicaudatus	WIDE	x	x	x	
Emballonura alecto	WIDE	x	x	x	
Taphozous melanopogon	WIDE	x	x	x	
Megaderma spasma	WIDE	x	x		
Hipposideros ater	WIDE			x	
Hipposideros diadema	WIDE	x			
Hipposideros obscurus	PHIL			x	
Rhinolophus arcuatus	WIDE	x	x	x	
Rhinolophus inops	MIND	x	x		
Rhinolophus rufus	PHIL	x			
Rhinolophus virgo	PHIL	x		x	
Harpiocephalus harpia	WIDE	x			
Kerivoula hardwickii	WIDE	x			
Miniopterus australis	WIDE	x			
Miniopterus schreibersii	WIDE	x			
Miniopterus tristis	WIDE	x			
Murina cyclotis	WIDE		x		
Myotis muricola	WIDE	x	x	x	
Philetor brachypterus	WIDE	x			
Scotophilus kuhlii	WIDE	x	x	x	
Chaerephon plicata	WIDE	x			
Primates					
Tarsius syrichta	MIND	x	reported	reported	
Macaca fascicularis	WIDE	x	x	x	
Rodentia					
Exilisciurus concinnus	MIND	x	x		
Sundasciurus samarensis	MIND	x	x		
Apomys littoralis	MIND	x	x		
Batomys salomonseni	MIND	x	x		
Bullimus bagobus	MIND	x		x	
Crunomys rabori	LEYTE	x			
Mus musculus†	WIDE	x		x	
Rattus everetti	PHIL	x	x	x	
Rattus exulans†	WIDE	x	x		
Rattus rattus†	WIDE	x	x	x	
Carnivora					
Paradoxurus hermaphroditus	WIDE	x	sign	sign	
Viverra tangalunga	WIDE	x			

TABLE 20. *Continued.*

	Distribution*	Leyte	Biliran	Maripipi	Totals
Artiodactyla					
Cervus mariannus	WIDE	x	reported		
Sus barbatus	WIDE	x	x		
Native species					
Non-volant species		15	10 (+ 2)	6 (+ 1)	15
Large fruit bats		4	(1)	3	4
Small fruit bats		9	9	7	9
Microchiroptera		17	8	8	20
All natives		45	27 (+ 3)	24 (+ 1)	48
Introduced species		4	2	2	4
All species		49	29 (+ 2)	26 (+ 1)	**52**

* Distributions (after Heaney et al., 1987): LEYTE = restricted to Leyte; MIND = restricted to Mindanao faunal region; PHIL = widespread in oceanic Philippines; WIDE = occurring outside of oceanic Philippines.
† Introduced commensal species.

typically have low population densities and thus require larger areas to sustain viable populations. We believe it likely that the absence of pigs and deer on Maripipi stems from natural extinction. However, it is certainly possible that both species may have become extinct through relatively recent hunting pressures.

Small mammals with restricted elevational ranges also appear to be susceptible to extinction on small islands, presumably because of narrower ecological tolerances. On Leyte, *Batomys salomonseni* was restricted to high-elevation forest, where it was the most frequently trapped species (table 1). However, it was rare in similar habitat on Biliran and was absent from Maripipi. The distribution of *Apomys littoralis* is suggestive of similar limitations. The situation for the widespread Philippine native rat, *Rattus everetti,* provides an interesting contrast. In surveys on Leyte (this study, table 1) and Luzon (Rickart et al., 1991), this species was common in habitats ranging from lowland dipterocarp forest to high-elevation mossy forest. Perhaps because of this broad ecological tolerance, it has survived on Maripipi, where more specialized species have not.

Ecological factors may also explain the distributional limitations of small fruit bats among these islands. Of the species that were common on Leyte and Biliran, *Haplonycteris fischeri* and *Ptenochirus minor* were conspicuous in that they were almost never encountered outside of forested habitats. This inability to tolerate disturbance may be associated with their apparent absence from Maripipi.

Netting and Trapping Success

Our field work on Leyte served as a basis for formulating several general predictions concerning patterns of variation in species richness and abundance of small mammals in Southeast Asia (Heaney et al., 1989). Subsequent studies generally have supported these predictions (Heaney & Rickart, 1990; Heaney et al., 1991; Rickart et al., 1991), and we believe that data from Biliran and Maripipi can be used to further test their generality.

The relevant predictions from Heaney et al. (1989) derived from our studies on Leyte and Negros are (1) in forested habitats, species richness and relative abundance of fruit bats should be highest in the lowlands and decline with increasing elevation, (2) species richness of fruit bats should be lower in agricultural areas, where geographically widespread species should predominate, (3) non-volant mammals should not exhibit highest species richness in lowland forest, (4) abundance of non-volant mammals should increase with elevation, and (5) endemic species of fruit bats and non-volant mammals should occur in primary forest, whereas non-endemics should predominate in disturbed habitats.

Data on species richness of small fruit bats on Biliran and Maripipi (table 5) generally support predictions 1 and 2. Species richness was highest at the lowest elevation forested sites (sites B2 and M1) and declined with elevation to reach lowest values in mossy forest. On both islands there was also an indication of a decline in relative abun-

dance with elevation (as measured by netting success). Species richness of fruit bats was comparatively low at the one agricultural site on Biliran (B1), and widespread non-endemic species were predominant there (table 5).

For non-volant small mammals, species richness was highest in middle- or high-elevation forest sites on both Biliran and Maripipi (table 1). This is in general agreement with prediction 3. Data pertaining to prediction 4 are somewhat equivocal. As on Leyte, relative abundance (as measured by trap success) reached a maximum in high-elevation mossy forest on Biliran. Musser and Heaney (1992) showed that this is also true on Mindanao. However, the opposite was true on Maripipi (table 1). This suggests that there are some fundamental differences in the structure of non-volant small mammal communities on very small land-bridge islands such as Maripipi. The most obvious effect may involve reduced species richness. Those rodent species that were most abundant at high elevations on Leyte and Biliran were not encountered on Maripipi, where high-elevation mossy forest is extremely limited. A striking difference between these islands involves the habitat associations of endemic and non-endemic species (prediction 5). On both Leyte and Biliran, endemic species of fruit bats were predominant in forested habitats but were rare or absent at disturbed sites, where widespread non-endemic species were most abundant (table 5). In contrast, two of the most abundant endemic species on Leyte and Biliran, *Haplonycteris fischeri* and *Ptenochirus minor,* were not encountered on Maripipi, and widespread non-endemic species (*Cynopterus brachyotis, Macroglossus minimus,* and *Rousettus amplexicaudatus*) were more common at some of the forested sites (table 5). Among non-volant mammals, native species were restricted to forested habitats on all three islands. On Leyte, commensal species were never encountered in primary forest. However, on both Biliran and Maripipi, the widespread commensal rat, *Rattus rattus,* was present and often abundant at forested sites (table 1).

The occurrence of widespread non-endemic or commensal species (such as *C. brachyotis* and *R. rattus*) in primary forest habitats on small land-bridge islands (such as Maripipi) resembles the situation on some large oceanic islands (e.g., Negros; Heaney et al., 1989; Heideman et al., 1987). The phenomenon is apparently associated with the relatively low species richness values characteristic of both types of islands. This leads us to suggest the hypothesis that non-endemic mammals in the Philippines are at a competitive disadvantage in areas that support rich endemic communities. This hypothesis, which is the opposite of what often is seen on New World islands (e.g., Morgan & Woods, 1986), clearly deserves careful testing.

Conservation

This study has dealt with only a small geographic area and but a fraction of the rich mammal fauna of the Philippines. Nonetheless, we believe that several general patterns emerging from this and other recent studies (Heaney et al., 1991; Rickart et al., 1991) have direct bearing on wildlife conservation issues in the Philippines as a whole.

First, the continued destruction of primary forest habitat constitutes the most direct threat to wildlife. On Leyte alone, approximately 90% of the primary forest has been lost in little more than a century (fig. 18). Deforestation has been highly patterned, progressing from lowland areas with the most accessible and commercially valuable timber and agricultural land to more remote areas at higher elevations. On Leyte, most of the remaining forest is now confined to areas above 500 m elevation and is highly fragmented. Given this pattern of progressive forest loss, the most vulnerable wildlife species are those that are restricted to low-elevation forest.

Second, there is a clear pattern of habitat association and endemism. Endemic species generally are restricted to areas with undisturbed or lightly disturbed natural vegetation (i.e., primary forest), whereas heavily disturbed habitats generally support only widespread or introduced species. Furthermore, abundance under pristine conditions may not be indicative of the ability of a species to tolerate disturbance. Any disturbance of natural habitat in the Philippines will therefore have a disproportionately greater negative impact on endemic portions of a local mammal fauna than on the widespread Asian component.

Third, species that are large or uncommon may

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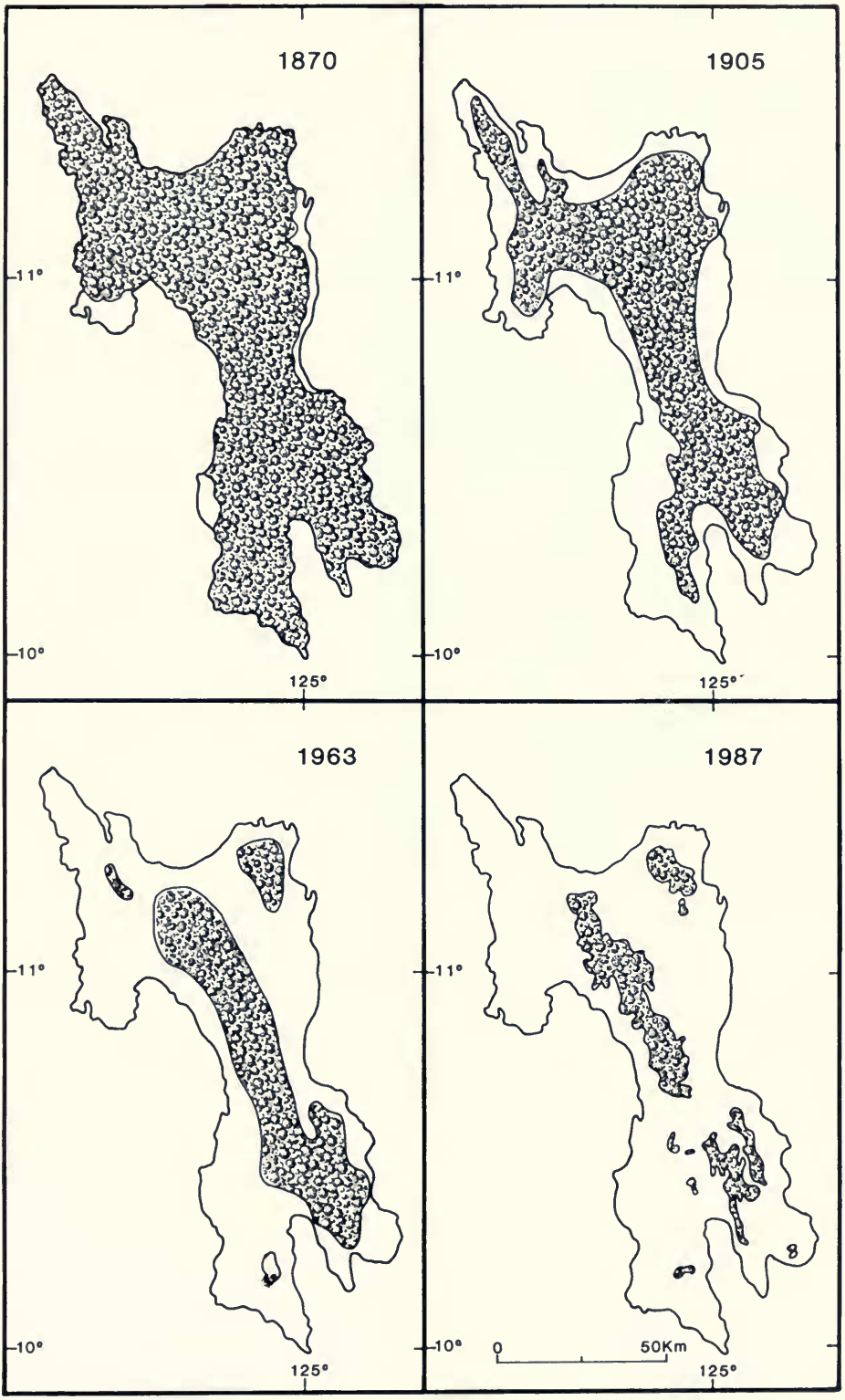
FIG. 18. Approximate extent of forest cover on Leyte in 1870, 1905, 1963, and 1987 (Sources: Anonymous, 1876, 1905; Huke, 1963; National Mapping and Resource Information Authority, 1988.)

Primary Forest on Leyte Island



exist at low population densities under natural conditions. To protect such species, parks and forest reserves need to be large enough for them to maintain viable populations. In this study, the absence from Maripipi of several species of bats, squirrels, and large mammals strongly implies that an isolated reserve would need to be larger than 22 km² (the area of Maripipi) in order to provide indefinite long-term protection.

Fourth, many species are restricted to particular habitat types or have limited elevational ranges. To protect entire faunas, reserves need to encompass broad elevational transects ranging from lowland dipterocarp forest to mossy forest. In the Philippines, highland areas are particularly important in that they generally support a large proportion of local endemics.

Fifth, many species have special ecological requirements. Such is the case with bats that roost in caves. Many of those species that have been reported from Leyte are rare or absent on Biliran and Maripipi, both of which lack large caves. Even on large islands, cave-roosting species are vulnerable to local extinction in the event of roost disturbance; such appears to have been the fate of *Chaerephon plicata* at Cathedral Cave on Leyte. Species that require both cave roosts and primary forest habitat are particularly susceptible (Heaney & Heideman, 1987).

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